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Justin R. DeRose

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R. Justin DeRose
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DISTURBANCE ECOLOGY AND VEGETATION DYNAMICS AT VARYING
SPATIAL- AND TEMPORAL-SCALES IN SOUTHERN ROCKY
MOUNTAIN ENGELMANN SPRUCE FORESTS

by

R. Justin DeRose

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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2009

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ABSTRACT

Disturbance Ecology and Vegetation Dynamics at Varying Spatial and Temporal Scales
in Southern Rocky Mountain Engelmann Spruce Forests

by

R. Justin DeRose, Doctor of Philosophy

Utah State University, 2009

Major Professor: Dr. James N. Long
Department: Wildland Resources

High-severity disturbances are the primary drivers of Engelmann spruce-subalpine fir ecosystems in the southern Rocky Mountain. Recently, an unprecedented, landscape-wide (at least 250 km²) spruce beetle outbreak killed virtually all the Engelmann spruce on the Markagunt Plateau in southwestern Utah, USA. Results from dendroecological analyses suggested the combination of antecedent disturbance history and drought-driven stand development was responsible for creating suitable host conditions prior to the recent outbreak. Multiple and consistent lines of evidence suggested mixed- and high-severity fires shaped the development of the Markagunt Plateau. Subsequent stand development, influenced by species-specific differential tree-ring response to drought, resulted in the gradual increase of Engelmann spruce dominance across the landscape.

Spatiotemporal outbreak dynamics included the early, independent and spatially synchronous building of beetle populations in moist sites with large Engelmann spruce across the landscape. As the outbreak evolved over time, it is likely temperature

anomalies accelerated beetle population growth, leading to more rapid spruce mortality. In the wake of the spruce beetle outbreak, results from simulated potential fire behavior suggested there was a reduction in probability of active crown fire for one or two decades on near-pure Engelmann spruce sites after the outbreak. This counterintuitive result suggested extreme fire behavior is not an inevitable consequence of spruce beetle outbreaks. Regardless of the occurrence of fire, forest response is likely to be dominated by advance regeneration in the seedling bank. Furthermore, because spruce was virtually absent from the understory, forest reorganization is likely to be dominated by subalpine fir.

In response to recent outbreaks such as the Markagunt Plateau, silviculturists are questioning what they can do to limit the loss from these likely inevitable spruce beetle outbreaks. Concepts of resistance and resilience can be used in planning vegetation management intended to indirectly control beetle populations by manipulating their habitat (vegetation). Resilient landscapes will ideally have spruce age class diversity and size class diversity in spatially discontinuous patches.

(181 pages)

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R. Justin DeRose

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CHAPTER 1

INTRODUCTION

Natural disturbances are important ecological processes that drive observed patterns in ecosystems. The study of disturbance regimes and their interactions has only recently become a central theme in ecology. Disturbance ecology topics that require further inquiry include: disturbance history, spatiotemporal dynamics, disturbance interactions, regeneration response to disturbance, and the application of resistance and resilience theory to ecosystem management. It is the intent of this research to further investigate these areas of interest.

During the 1990s a landscape-wide spruce beetle outbreak killed virtually all the Engelmann spruce (*Picea engelmannii*) on the Markagunt Plateau in southwestern Utah. Because it was only recently killed, the pre-outbreak spruce forest could be reconstructed to answer questions regarding (1) What was the role of antecedent disturbances in the recent outbreak? (2) What were the spatiotemporal dynamics of spruce mortality during the outbreak? (3) What is the potential for interaction between spruce beetle outbreaks and subsequent wildfire? (4) What is the role of biological legacies on the regeneration response to spruce beetle outbreaks? Taken together, new knowledge accumulated as a result of examining these questions will lead to novel approaches that consider resistance and resilience in the context of ecosystem management.

CHAPTER 2

INFLUENCE OF ANTECEDENT DISTURBANCES AND DROUGHT ON A
LANDSCAPE WIDE SPRUCE BEETLE OUTBREAK IN THE SOUTHERN ROCKY
MOUNTAINS ¹

Abstract

In the subalpine forests of the Rocky Mountains, high-severity disturbances affect stand dynamics and vegetation patterns; however, less is known about how disturbances might directly or indirectly influence the probability of a subsequent disturbance event. Recently, an unprecedented, landscape-wide (at least 250 km²) spruce beetle outbreak killed virtually all the Engelmann spruce on the Markagunt Plateau in southwestern Utah. Dense spruce forests dominated the landscape prior to the outbreak giving the impression that in the past a similar large-scale disturbance might have resulted in the regeneration of the spruce-dominated forest that ultimately succumbed to the mid-1990s outbreak. In this study, we sought to investigate the possible influence previous disturbances had on the recent spruce beetle outbreak by reconstructing disturbance histories using dendroecological data from 11 sites on the Markagunt Plateau. Results suggested the combination of disturbance history and drought-driven stand development was responsible for creating suitable host conditions for the recent spruce beetle outbreak. Multiple and consistent lines of evidence suggested mixed- and high-severity fires that occurred during times of drought initiated and shaped the development of Engelmann spruce-dominated stands across the entire plateau. Unlike the recent outbreak, there was

¹ Coauthored by R. Justin DeRose and James N. Long

little synchrony between sites suggesting the fires were not landscape-wide events. Subsequent stand development, which was influenced by species-specific differential response to drought, resulted in the gradual increase of Engelmann spruce homogeneity across the landscape. The mechanism for this was the favorable response, as evidenced by tree ring release, of drought-tolerant Engelmann spruce to periods of above average moisture conditions when compared to subalpine fir. Based on our results, we speculate differential drought-tolerance as a mechanism for spruce-fir coexistence in subalpine forests of southwestern Utah.

INTRODUCTION

Disturbances affect forest vegetation structural and compositional dynamics which, in turn, ultimately influence the ecological effects of, and susceptibility to, subsequent disturbance. In the subalpine forests of the Rocky Mountains high-severity stand-replacing fire, catastrophic wind, and spruce beetle (*Dendroctonus rufipennis* Kirby) outbreaks are the most dramatic disturbances. By creating fundamentally different structures and compositions (DeRose and Long 2007) these disturbances directly affect relatively small scale stand dynamics (Veblen et al. 1991a), shape large scale landscape patterns (Turner et al. 1994), influence the degree of forest heterogeneity at multiple spatial scales (Schoennagel et al. 2008), and indirectly influence the probability of subsequent disturbances (Bebi et al. 2003, see Chapter 4).

Extreme climatic conditions also have a direct effect on the occurrence of disturbances (Bessie and Johnson 1995), and an indirect effect on stand dynamics through their influence on individual trees (Breda et al. 2006). Moisture deficit (i.e., drought) is

thought to predispose forests to high-severity fires or spruce beetle outbreaks whereas windstorms may result in large scale wind throw events (Everham and Brokaw 1996). The indirect effects of climate may influence stand development processes such as establishment (Little et al. 1994), growth (Zhang et al. 1999) and mortality (Johnson et al. 1994). For example, climatic variation in moisture and temperature results in species-specific differential growth rates (Villalba et al. 1994), and drought has been shown to cause lagged tree mortality of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and to a lesser extent Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) in the Colorado Rocky Mountains (Bigler et al. 2007). In contrast, moisture excesses (i.e., pluvial) are partly responsible for ‘increasing tree densities and fuel loads in western forests that subsequently can burn catastrophically’ (Goforth and Minnich 2008).

To the extent climatic conditions and antecedent disturbance interact to influence subsequent disturbance is not well understood; however multiple interaction scenarios among high-severity disturbances have been postulated and might predictably be influenced by climate. For example, changes in fire potential after severe blowdown or spruce beetle-caused mortality (Knight 1987, McCullough et al. 1998, see Chapter 4) are likely heavily influenced by drought, whereas decreased fire potential after fire (Bigler et al. 2005) is probably most heavily influenced by restructured stand conditions. Reported increases in the probability of spruce beetle outbreaks after fire or blowdown (Bebi et al. 2003) might have been influenced by drought, physiologic host changes, or structural changes to the host (i.e., from live standing to dead and down).

Ecological stand demographic patterns (Brown and Wu 2005), and their associated relationships with climate, can help elucidate the type of disturbance that initiated and

shaped the development of the stand. Differences in age and size structure, composition, and tree ring increment reflect vegetation responses to wildfire, catastrophic wind events, or spruce beetle outbreaks. Response to stand-replacing fires in the subalpine zone is not species-specific, typically results in the rapid recruitment of shade-intolerant species, and commonly occurs during periods of extended drought (Bessie and Johnson 1995). As a result of the opening of growing space and little competition from overstory remnants, fires are characterized by:

- Peaks in establishment of shade-intolerant pioneers or species that establish in mineral soil,
- Rapid initial tree ring increment of new recruits,
- Tree-ring release of remnant trees.

Response to large scale blow-down is also not species-specific and typically only affects larger, overstory trees. Whereas, nearly all subcanopy and understory trees are not negatively affected and their response is characterized by:

- Possible peaks in establishment of shade-intolerant species,
- Tree ring release and canopy accession of subcanopy and understory trees.

Response to spruce beetle outbreaks, however, is species-specific and typically affects larger diameter Engelmann spruce (>10 cm, Schmid and Frye 1977). As a result, the established understory and subcanopy trees when present, are released (see Chapter 5, and response is characterized by:

- Possible peaks in establishment of non-host species,
- Tree ring release and canopy accession of subcanopy and understory trees,
- Tree ring release of remnant trees.

In addition, many site variables such as: slope, aspect, fuel loading, site potential productivity, presence of charcoal, and presence of pit and mound topography can potentially aid in reconstructing past disturbances.

In the mid-1990s an unprecedented, landscape-wide (at least 250 km²) spruce beetle outbreak began on the Markagunt Plateau in southern Utah (DeRose and Long 2007) and did not subside until the host resource was exhausted. Prior to the outbreak extensive tracts of mature, dense spruce forest dominated the landscape which allowed the beetle to spread across the entire forest in approximately one decade. This observation gives the impression that the recent outbreak was a natural disturbance, and that in the past a similar landscape-extent disturbance might have resulted in the regeneration of the spruce-dominated forest that ultimately succumbed to the mid-1990s outbreak.

In this study we explored how reconstructed antecedent disturbances and climatic activity influenced the creation of landscape-wide susceptible host conditions necessary for the outbreak. To do this we reconstructed disturbances histories for 11 sites across the Markagunt Plateau. The role of climate on reconstructed disturbance history, subsequent stand development, and ultimately on the recent outbreak were assessed by comparing them to the regional drought cycle. Analysis of disturbance histories, their synchrony between sites, and the effect of climate revealed to what extent these variables influenced the subsequent landscape-wide outbreak.

STUDY AREA

The Markagunt Plateau is located on the Cedar City Ranger district of the Dixie National Forest in southwestern Utah, and has a high proportion of southern Rocky

Mountain subalpine spruce-fir forests. We selected 11 sites across the Markagunt Plateau (Fig. 2.1) to characterize the high elevation spruce-fir forest (Table 2.1). The number of plots within each site varied depending on total stand size. Sites were chosen to represent the range of spruce-fir conditions that existed on the plateau immediately prior to the 1990s spruce beetle outbreak and species composition ranged from nearly complete spruce dominance to mixed-conifer that was dominated by spruce and fir (Table 2.2). Species associated with southern Rocky Mountain spruce-fir forests are, in order of representation in this study: aspen (*Populus tremuloides* Michx.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), limber pine (*Pinus flexilis* James), and to a much lesser extent white fir (*Abies concolor* (Gord. And Glend.)), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws). Lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.), while often a component of spruce-fir forests in the Intermountain West does not occur on the Markagunt Plateau which is outside the lodgepole pine southwestern range limit. Engelmann spruce was the oldest tree on every site except for Bristlecone Pine Trail and Navajo Lake where overstory Douglas-fir were similarly old (Table 2.1). Precipitation comes mostly as snow but also as southwestern monsoon rainfall during the summer (see Fig. 4.1 in Chapter 4) and annual averages vary between 368 and 1709 mm. Strong historical fluctuations in drought/pluvial cycles are evident in the Palmer Drought Severity Index (PDSI) reconstruction (grid point 87, Cook and Krusic 2004) for the region, which fluctuated annually from -6.151 to +4.652. PDSI effectively characterizes long-term drought periods (months to years) where 0 is normal negative numbers are drought periods and positive numbers are pluvial periods. The period of observation in this study (1480-2000) includes the largest drought (mega-

drought, 1571-1586,) and largest pluvial (1905-1917) of the last 500-700 yrs (Stahle et al. 2007). The geologic substrate varies widely across the plateau owing to large intrusions of relatively young (Holocene) basalt lava flows, which occur within a matrix of much older (upper Cretaceous) formations composed of primarily sedimentary material, i.e., sandstones, mudstones, and limestones (Moore et al. 2004).

METHODS

Field methods

At each site, plots were located on a systematic grid with a random starting point. Variable radius prism plots were employed to characterize structure and composition on each plot and to indicate which trees would be cored. The number of plots on which structure, composition, increment cores, fuel loads, and charcoal data were measured varied (Tables 2.1, 2.2, and 2.3). In each plot all live and dead standing trees > 5 cm diameter at breast height (DBH, 1.3 m) were assessed for species, status (alive, dead, cause of mortality), DBH, and height. Since the recent beetle outbreak began in the early 1990s and had exhausted the host resource by ~ 2001 nearly every beetle-killed spruce was still standing (~99.2%, see Chapter 5 and were easily identified as beetle-killed or otherwise, and whether they died prior to or during the outbreak. To determine whether the spruce beetle was the cause of mortality we noted the presence of emergence holes, recent beetle galleries, and sloughing bark. To reconstruct spruce crown lengths, height to the base of the putative live crown was determined by visually assessing the lowest branches for evidence of fine twigs, indicating the branch had been living prior to beetle

attack. Height to the base of the live crown for spruce determined to have died prior to the outbreak was not measured.

To determine tree ages, tree ring increment, and initial growth increment cores were taken from each tree > 5 cm DBH on a subsample of the plots in each site. Cores were removed as low as possible on the tree bole, typically ~5 – 20 cm above the ground, and the increment bore angled downward in an attempt to intersect the pith at ground level. Trees were repeatedly cored until the pith or near-pith sample was attained, evident by curvature in the rings. No adjustments were made to age trees to reflect this type of sampling; therefore, although we attempted to measure actual tree ages they are interpreted as age at coring height. Because of the near complete spruce mortality on our study area (>95%, DeRose and Long 2007), in addition to the plot level increment cores, we opportunistically cored any large, living spruce we encountered so that the beetle-killed spruce could be crossdated.

Understory trees were measured on fixed-area plots (1.0 – 3.0 m radius) at the center of a subsample of the overstory plots. Detailed methods are in Chapter 5; briefly, species, height, and diameter at root collar were recorded before a cross section at ground level was removed to determine tree age.

Tree-ring measurement

Increment cores and understory cross sections were prepared and processed using standard dendrochronological methods (Stokes and Smiley 1968). Tree rings were measured to the nearest 0.001 mm using a stereo microscope. Crossdating was done by constructing local, species-specific chronologies from the larger, live individuals in our

plots and using those to date the remainder of trees. To anchor the dead Engelmann spruce cores to calendar years, an existing local chronology (K. Briffa and F.H. Schweingruber, World Data Center for Paleoclimatology Data Contribution, [sic] Cedar Breaks Engelmann spruce chronology, NOAA/NCDC Paleoclimatology Program, Boulder, Colorado, USA²) was combined with our live, opportunistically cored spruce and an up to date chronology developed. We then established the last year of ring increment (presumably date of death, *sensu* Mast and Veblen 1994) for spruce beetle-killed trees. Program COFECHA (Holmes 1983) was used to check for measurement and dating errors. For the rare tree species, ring dates were checked against the Engelmann spruce chronology. For cores that did not intersect the pith Duncan's (1989) method was used to estimate the number of rings (up to 25) to the center. Some of the trees were too rotten to core, would not crossdate, or had > 25 rings to the center, and were not included in the age structure or early growth analyses. Of the 1,171 trees cored in the field, 888 were successfully crossdated (62% spruce, 26% fir, 8% aspen, 4% other), within 25 yrs of the pith, and used to build age structures and to determine initial rapid growth.

Evidence of antecedent disturbances

To reconstruct antecedent disturbances, multiple lines of evidence were investigated including tree ring-based methods (age structures, tree ring release dates, initial growing conditions), and field observations (percentage charcoal, pit and mound topography, and fuel loading). For this study 'current' stand conditions were reconstructed to represent the forest immediately prior to the recent spruce beetle outbreak (mid-1990s). Therefore,

² URL: <http://www.ncdc.noaa.gov/paleo/treering.html>

stand structure, composition, age structures, tree ring increment, and ~99% of the understory (see Chapter 5) represented the mid-1990s spruce forest. Although we initially sought fire-scarred trees to corroborate fire dates, we virtually none in the spruce-fir forests on the plateau.

Age structures

Static age structures are a common way to infer stand history. Although criticisms such as ‘loss of evidence over time’ (Johnson et al. 1994) have been suggested, in some systems (e.g., moist spruce-fir) it is the primary way demographic histories are reconstructed (Kulakowski and Veblen 2006). Because of a paucity of fire-scarred trees careful interpretation of age structures is the best way to reconstruct spruce-fir stand histories (except on dry, exposed sites that are not representative of moist spruce-fir communities, *sensu* Sherriff et al. 2001). Some common age structure patterns in spruce-fir forests include peaks in species-specific establishment which might indicate response to high severity disturbances such as fire. Alternatively, long, drawn-out establishment might indicate conditions after low severity disturbances such as canopy gaps created by endemic bark beetle populations or wind. The synchrony of these events across sites might be evidence of larger scale disturbances (i.e., spruce beetle outbreaks).

To build age structures the number of trees that established per decade was standardized by current (pre-1990s outbreak) site occupancy and averaged over the number of plots where trees were cored at each site (Table 2.2). Site occupancy was defined as a function of each individual tree’s contribution to overall stand leaf area. Stand density index was used as a proxy for leaf area since it is directly proportional

(Long and Dean 1986). Therefore, frequency of site occupancy (Fig. 2.3) simultaneously depicts decade of origin of trees and their current dominance in the canopy in terms of leaf area. Age structures at each site were scrutinized plot by plot to ensure the disturbance signal was not driven by a few plots but rather characterized the site level forest response. Trees that established prior to age structure peaks were interpreted as remnants that survived the putative disturbance (*sensu* Kulakowski and Veblen 2006). Because site productivity potential can aid interpretation of age structures (D. Kulakowski, personal communication) site index was calculated using the heights and ages of the 10 tallest spruce at each site (Alexander 1967) (Table 2.1).

Tree-ring release

To determine the percentage of trees released by species per year for all canopy and subcanopy trees at each of the sites, species-specific tree ring series were standardized using the series mean. Instead of removing growth related trends from tree ring series, typically sought by dendroclimatic studies, mean standardization emphasized variation in tree ring increment through time which was necessary to detect increases in ring width associated with recently improved growing conditions e.g., loss of canopy trees as a result of disturbance. This method has been found to be highly effective when detection of canopy disturbance is sought (Eisenhart and Veblen 2000). After extensive preliminary investigation a release was defined as 100% increase in average ring width over five years compared with the five years immediately prior. Although liberal compared to other studies (Veblen et al. 1991c), these release criteria were necessary for two reasons: 1) releases of > 100% or groups of > 5 years resulted in nearly no tree ring releases for

complacent Engelmann spruce, and 2) because climatic influence on growth patterns was sought, we did not try to remove the influence of the drought cycle on tree ring releases. A 10 year time-lag was used to reduce autocorrelation, i.e., so that a tree recording a release could not record another release for 10 years. Sampling depth was compared with the release data to ensure peaks in release were not due to rapidly increasing sample sizes that would have indicated a peak of regeneration in response to a smaller-scale disturbance event. We found these criteria appropriate for all species in the analysis. Site and species-specific releases were calculated using program JOLTS (R.L. Holmes, unpublished). Tree ring releases used in subsequent analyses and in constructing graphics were calculated for the portions of the chronologies with > 5 trees. In addition to the 11 sites sampled for this study, tree ring widths from three previously measured sites (DeRose and Long 2007), which had a nearly identical sampling protocol, were included in the release analysis.

Initial growing conditions

Increment cores were analyzed separately for growing conditions immediately following the establishment of the overstory trees, which were determined from the pattern and width of ring increment from the pith outward. We adopted the definition proposed by Parish et al. (1999) for rapid initial growth of Engelmann spruce; > 1 mm per year for a continuous period of 10 years that occurred during the first 25 years after establishment. We then tallied overstory trees by whether they had initial rapid growth or not on a site by site basis. Then a frequency distribution by decade that included all species was calculated and juxtaposed over age structure for each site so that a

simultaneous examination of rapid early growth and peaks in establishment could be viewed. We assumed that rapid early growth coupled with increases in establishment were indicative of response to high-severity disturbances, whereas continuous or variable early growth and establishment would indicate response to low-severity disturbances.

Corollary evidence of disturbance

Besides demographic data, site level information that might indicate past disturbance was collected. To evaluate the historical influence of wind throw, pit and mound topography was assessed using eight 100 m transects laid out in randomly determined directions at each site. The length of transect that intersected pit or mound was measured and averaged for the site. To determine the possible historical role of fires, the forests soil was inspected at 3 m intervals for the presence/absence of charcoal. Charcoal data were averaged across plots for a site level percentage. Because the quantity of fuel on the forest floor is an indicator of time since last fire, total fuel loading was determined using the standard planar intersect method (Brown et al. 1982), detailed in (see Chapter 4).

Influence of climate on establishment and stand development

Preliminary graphical analyses indicated a probable association between overstory establishment, tree ring releases, and understory establishment with chronic drought cycles characteristic of the West (MacDonald and Tingstand 2007). To characterize drought we used the tree ring reconstruction of the long-term (20-yr long-pass filter) PDSI for grid point 087 (Cook and Krusic 2004). The long term record was used instead of the annual data because rapid year to year changes in moisture conditions would be attenuated leaving an interannual pattern of increasing and decreasing moisture with

easily defined ‘peaks’ and ‘troughs’. The long-term pattern of drought conditions is more likely to explain phenomena such as high-severity disturbance and subsequent stand development than the year to year record because high-severity disturbances such as fire in spruce-fir forests commonly occur after extended periods of drought (Bessie and Johnson 1995). Similarly, episodes of tree mortality and growth release of survivors as a result of fluctuation in drought conditions are unlikely to occur within a given year rather, these aspects of stand dynamics proceed over many successive years (Parish et al. 1999, Bigler et al. 2007). To infer whether putative fire events were the result of dry conditions, decades of overstory establishment were graphically assessed for their coincidence during, or immediately following, a trough in PDSI (e.g., 1780-90, Fig.2. 2).

The presence or absence of tree ring release during alternating drought cycles was analyzed. A composite of the long-term PDSI record was built based on whether it was increasing (trough to peak) or decreasing (peak to trough) (Fig. 2.2). Similarly, for each species at each site, and for the record of tree ring release with > 5 trees, composite of the presence or absence of a release was made. Subsequent counts were made of: 1) release during increasing moisture, 2) release during decreasing moisture, 3) absence of release during increasing moisture, and 4), absence of release during decreasing moisture. The length of the tree ring chronologies were different for each species by site combination and defined the time period over which the counts occurred. Two by two contingency tables for each species at each site with sufficient sample size (Agresti 1990) were populated with these counts and the chi-square test for homogeneity of proportions was used to test the null hypothesis that the observed number of tree ring releases during ‘increasing’ or ‘decreasing’ moisture condition was not different than chance. The

Cochran-Mantel-Haenszel test for homogeneity of odds ratio was used to simultaneously analyze multiple contingency tables and was calculated to reduce the results to a species-specific, cross-site statistic (Agresti 1990).

The understory establishment data were also analyzed against a composite PDSI record. However, the composite was separately calculated four different ways: 1) increasing moisture conditions, 2) decreasing moisture conditions (similar to tree ring release above), 3) 'peaks' in PDSI, defined as the year of the peak \pm 3 yrs, and 4) 'troughs', defined as the year of the lowest point \pm 3 yrs. Counts of the presence or absence of understory regeneration, on a site and species-specific basis, were then performed during the presence or absence of each of the drought groupings. The time period of analysis varied for each species and site combination and was defined as beginning and ending during the years of the first and last observation of understory establishment, respectively. Two by two contingency tables were populated and analyzed similar to the tree ring data. We tested the null hypothesis that the observed species-specific regeneration did not differ from chance for each of the four PDSI composites.

RESULTS

Overstory establishment

Establishment peaks, a high percentage of initial rapid growth, and tree ring release of remnant trees on 5 of the 11 sites suggested high-severity fire was the putative antecedent disturbance, whereas 6 of the 11 sites had larger variation in establishment and early growth, but also had tree ring release of remnants, which suggested mixed-severity fire was likely the putative disturbance (Fig. 2.3). Peaks in spruce, and sometimes aspen

establishment, coupled with high percentages of initial rapid growth suggested high-severity fire occurred at Hancock Peak Trail, Lava Cone, Navajo Lake, Snotel, and Sydney Valley ca. 1680s, 1680s, 1770s, 1650s, and 1800s, respectively (Fig. 2.3). These putative dates of antecedent fire were coincident with dry conditions (PDSI) for Navajo Lake (see Fig. 2.2 as an example), Snotel, and Sydney Valley, but not for Hancock Peak Trail or Lava Cone. Putative fire dates were also coincident with tree ring release of remnant spruce that survived the fire on Lava Cone, Navajo Lake, and Snotel (Fig. 2.4). In contrast, high-severity fires at the Hancock Peak Trail and Lava Cone sites probably occurred during relatively moist conditions but interestingly were during the same decade and might indicate the same fire event given their relative proximity (Fig. 2.1 and 2.3). Percent charcoal found at the steep, north facing, high site index sites (Snotel and Navajo Lake) was high, which further supported the role of fire, whereas for the other, south facing, sites results were variable (Tables 2.1 and 2.3).

At Ashdown, Bristlecone Pine Trail, North Hancock, Midway Point, Mammoth Creek, and Rainbow Meadows patterns of establishment and initial rapid growth were more variable than the previous five sites and indicated a more likely history of mixed-severity fire during, ca. 1720s, 1740s, 1730s, 1880s, 1830s, and 1860s, respectively (Fig. 2.3). Dry conditions were coincident with these putative fire dates on all sites except Ashdown and Mammoth Creek where conditions were moist prior to establishment (Fig. 2.3). Tree ring release suggested putative fire dates on Ashdown, North Hancock, Midway Point, Mammoth Creek, and Rainbow Meadows (Fig. 2.4). There was synchrony in establishment during the 1870-80s between Sydney Valley, Rainbow Meadows, and Midway Point, which coincided with the arrival of sheepherding settlers (Sampson 1923).

Regardless of the differences in patterns of establishment, nearly all sites had four things in common: 1) high- or mixed-severity fire was likely the antecedent disturbance, 2) substantial numbers of remnant trees pre-dated the putative antecedent disturbance and commonly these were spruce, 3) relatively chronic establishment of overstory spruce up until the 19th century, when increasing subalpine fir was detected (Fig. 2.3) and, 4) with the exception of Sydney Valley and Rainbow Meadows, all sites were strongly dominated by spruce (Table 2.2).

Stand development

Subsequent to stand initiation, patterns of continued establishment and tree ring release characterized stand development. While Engelmann spruce had relatively continuous establishment at all sites, subalpine fir and aspen establishment was not measured until later owing to their shorter life spans (Fig. 2.3). Subalpine fir established as early as the mid-1600s (e.g. Snotel) and has chronically regenerated since (Fig. 2.3). Aspen however established in pulses, often coupled with a peak in initial rapid growth (e.g., Midway Point ca. 1880, Mammoth Creek ca. 1830, and Rainbow Meadows ca. 1870) (Fig. 2.3), indicating its reliance on higher severity disturbances to regenerate.

Patterns of tree ring release generally varied by site and species; however, graphical analyses suggested they were associated with periodic drought. We failed to accept the null hypothesis based on the chi-square test, which indicated both Douglas-fir and Engelmann spruce were significantly more likely to release during periods of increasing moisture (Table 2.4), while subalpine fir and aspen did not differ from chance (Table 2.4). Therefore, synchrony in tree ring release of Douglas-fir and Engelmann spruce was

probably driven by pluvial periods. Synchrony in tree ring release between species within sites was found (e.g., Navajo Lake ca. 1880-1890 and Sydney Valley ca. 1900-1910, Fig. 2.4) and was almost always associated with conditions of increasing moisture (PDSI in Fig. 2.2). In contrast, release in response to the 1990s outbreak, depicted at nearly all the sites, and evident in all species (Fig. 2.4), was not associated with increasing moisture conditions (PDSI in Fig. 2.2). The combined magnitude and density of trees released as a result of the 1990s outbreak was not matched anywhere else in the tree ring record, which suggested a historic landscape-wide beetle outbreak was not detectable in our data (Fig. 2.4).

Regeneration establishment

In an earlier study we found chronic regeneration characterized the spruce-fir forests on the Markagunt Plateau. Furthermore, we measured understory establishment as early as 1805 (Ashdown) and, although composition and diversity of the understory varied by site, it was dominated by subalpine fir, which had notably increased in understory dominance over the past two centuries (see Chapter 5). An important exception to this was a pulse in aspen establishment immediately following the 1990s outbreak (see Chapter 5). Chi-square tests suggested we reject the null hypothesis, for subalpine fir, which was more likely to establish in the understory during times of decreasing moisture and less likely during peaks or troughs in PDSI (Table 2.5). In contrast, aspen was more likely to regenerate in the understory during peaks in moisture conditions (Table 2.5). Interestingly, Engelmann spruce understory establishment did not differ from chance for any of the drought combinations we tested (Table 2.5).

DISCUSSION

On the Markagunt Plateau, multiple and consistent lines of evidence suggested high- and mixed-severity fires were likely the dominant antecedent disturbances that originally regenerated the sites which ultimately succumbed to the recent landscape-wide spruce beetle outbreak. Variability in both the species and the timing of establishment, in combination with the limited synchrony between all sites and species, suggested antecedent disturbances were site specific and not a landscape-wide phenomenon like the recent spruce beetle outbreak. It is unlikely an outbreak of this magnitude has occurred in the history of these sites, and if spruce beetle activity had occurred it was much less severe. Rather, the individual stands likely originated from different disturbance regimes and then, in the absence of high-severity disturbances for the last few centuries, stand development processes pushed the landscape towards increasing spruce homogeneity where stand conditions highly susceptible to spruce beetle converged. Furthermore, antecedent disturbances and subsequent stand development both shared a strong relationship with drought cycles. In general the reconstructed putative fire events, which promoted Engelmann spruce establishment, likely occurred during or immediately following drought, while during subsequent stand development, chronic drought cycles promoted Engelmann spruce tree ring release to the detriment of subalpine fir. Therefore, the combination of disturbance history and drought-driven stand development were responsible for creating suitable host conditions for the recent landscape-wide spruce beetle outbreak.

Antecedent disturbances

It is likely that high- and mixed-severity fire regimes characterized antecedent disturbances in the spruce-fir forest on the Markagunt Plateau and resulted in the establishment of Engelmann spruce and to a lesser extent Douglas-fir and aspen that was coincident with initial rapid growth, and generally occurred during or immediately following drought conditions. Subsequent stand development was characterized by continued, albeit decreasing recruitment of Engelmann spruce and eventual increasing representation of subalpine fir, likely due to canopy accession from chronic understory regeneration. Overall the bulk of the evidence from our sites is consistent with well-known patterns of establishment and stand dynamics following stand-replacing fires and, although the timing varied between sites, time since disturbance was on the order of centuries suggesting all stands had very old origins in general. However, given the stand ages and fuel loading it is likely historical high- and mixed-severity fires were rare (return interval of many centuries) (Table 2.3). Because using stand origin to indicate fire dates is imprecise (*sensu* Kulakowski and Veblen 2006) our observation that most high-severity fires followed very dry conditions is somewhat speculative. However, in our study establishing exact fire dates was not the goal, rather we sought to determine whether the peaks of tree recruitment that likely indicated response to high-severity fire were coincident with drought conditions and whether they and subsequent stand development influenced the recent beetle outbreak. Although chi-square tests for homogeneity of proportions were conducted for tree ring release and understory regeneration dates at an annual resolution, the imprecise nature of establishment dates

(decadal not annual resolution, Fig. 2.3) from overstory trees were not conducive to the same analysis.

Had the antecedent disturbance been a conventional spruce beetle outbreak we would expect to see a seedling bank release of spruce and fir (Mielke 1950). Furthermore, a landscape-wide outbreak would be noticeable in the synchronous tree ring release of any remnant spruce and non-host species across all sites. In contrast, we observed a peak of establishment followed by decades of generally decreasing spruce establishment that would typically characterize response to fire. Many remnant trees, commonly spruce, pre-dating the putative antecedent disturbances are further evidence that a beetle outbreak like the one which occurred during the 1990s did not occur in the past. Had there been a landscape wide beetle outbreak similar to the 1990s there would have been few if any remnant spruce to rapidly colonize sites (see Chapter 5). Previous studies used objectively sampled, large Engelmann spruce to reconstruct past spruce beetle outbreaks and, when compared against independent chronologies to remove the influence of climate, found both historically documented and putative outbreaks (Eisenhart and Veblen 2000). In this study, all randomly located overstory trees (> 5 cm DBH) were used in the chronologies, which could partially explain the strong tree ring complacency of spruce that led us to use a less conservative tree ring release criteria than previous studies (we used 100% with 5 yr running mean versus 200-250% with 10-yr running mean) (Veblen et al. 1991c, Eisenhart and Veblen 2000). Because our sample was dominated by large spruce, and because we used a liberal release criterion, it is unlikely the results would change substantially by analyzing only the larger trees.

Had the antecedent disturbance been dominated by high-severity wind disturbance we would expect to see gradual accumulation of subalpine fir over time. Wind damage is not particular to species composition, usually blowing over mature canopy trees (Everham and Brokaw 1996), resulting in a release of all lower story trees, commonly shade-tolerant spruce and fir (Kulakowski and Veblen 2003). Historical evidence of wind, i.e., pit and mound topography, covered a very small percentage of the Markagunt Plateau landscape probably because wind thrown trees are usually broken off at the bole after being weakened by root and butt rots and rarely create pits or mounds (Table 2.3 and Mielke 1950). As a result wind damage likely does not typically result in the microsite conditions necessary for Engelmann spruce establishment (mineral soil seedbed) and probably played a small disturbance role historically on the plateau.

The remnant spruce were helpful in determining antecedent disturbances since their tree ring release was often coincident with putative fire events. Past studies have used the presence of many remnants as evidence of lower fire severity (Kulakowski and Veblen 2006). Indeed, many conditions similar to those described by Kulakowski and Veblen (2006) characterize the Markagunt Plateau, such as higher elevations and mesic sites with generally subtle topographic relief (Table 2.1). The sites with steep slopes (Navajo Lake and Snotel) had the clearest fire signal and highest percentage of charcoal (Fig. 2.3, Table 2.3) likely indicating higher fire severity. In contrast, it is likely fire severity on the rest of the plateau was more variable. A relationship between remnant trees and drought can also be drawn from our data. Few remnant spruce became established prior to the mega-drought (pre-1570, Fig. 2.3), and even fewer established during the mega-drought, whereas nearly all the remnant, drought-tolerant Douglas-fir (Navajo Lake and

Bristlecone Pine Trail) established during the mega-drought. Following the mega-drought (post-1600s) there was little Douglas-fir establishment; however, Engelmann spruce establishment occurred on more than half the sites (Fig. 2.3), although the timing varied by more than a century. We cannot determine whether the maximum stand ages of ~500 yrs were a result of the longevity of spruce or whether it indicated a response from previous disturbance; however, the timing is suggestive given the regional evidence for the late 16th century mega-drought (Brown and Wu 2005, Stahle et al. 2007).

An immediate peak in recruitment followed by drawn out establishment after disturbance is a widely documented pattern for Engelmann spruce forests. For example, Knowles and Grant (1983) described net recruitment of Engelmann spruce as climax after ~210 yrs (their Fig. 3) where ~10% of the total spruce were 200-500 yrs in age. Their analysis showed the 217 trees they measured were distributed across the 500 yr maximum age with no more than three per year. In a graphic of age structure this would appear similar to relatively continuous post-fire recruitment (e.g., Snotel, Fig. 2.3). Kulakowski and Veblen (2006) detected continuous post-fire establishment of Engelmann spruce that often lasted well over a century, which was similar to many of our sites. The drawn out establishment is likely due to the shade tolerance of spruce (Fiedler et al. 1985) in contrast to species like lodgepole pine or aspen which exhibit very short (i.e., less than a decade) peaks in post-disturbance recruitment because they are very shade-intolerant. Like Engelmann spruce, it is possible subalpine fir and aspen were present from the origination of the stand (e.g., subalpine fir was part of the Snotel post-fire cohort, ca. 1640, Fig. 2.3) but could not be detected by dendrochronological

techniques until after the establishment of currently extant individuals due to their shorter life spans.

Establishment patterns of remnant Engelmann spruce are less clear; however, if the cause of Engelmann spruce establishment from our understory data (Table 2.5) reflects the cause of establishment of the overstory remnants (Fig. 2.3) we can deduce that when remnant Engelmann spruce slowly grow into the overstory without rapid initial growth it is indicative of slow canopy accession from advance regeneration. This was likely the case for many of the remnant spruce (e.g., Mammoth Creek, Midway Point, Navajo Lake, North Hancock, Snotel, Fig. 2.3) and would occur periodically based on the response of the understory spruce to drought conditions (Table 2.5). The remnant spruce that established coincident with some initial rapid growth (e.g., Ashdown, Hancock Peak Trail, and Rainbow Meadows), although minimal, might indicate previous, partially stand-replacing disturbances or isolated spruce establishment in rare canopy openings.

Sydney Valley and Rainbow Meadows, which were not dominated by spruce, were still affected by the recent beetle outbreak. Interestingly, both Sydney Valley and Rainbow Meadows were south-facing, relatively young stands, suggesting time since fire might be influenced by aspect such that younger south-facing sites are likely to burn more often than their north-facing counterparts. Furthermore, the putative increased fire frequency on these south-facing sites would be further exacerbated during drought conditions. That aspen was generally much more predominant in south-facing sites suggests that it was more likely to respond favorably to stand-replacing fire than spruce or fir. Putative post-fire dominance by aspen would make it difficult for Engelmann spruce to regenerate (lacking mineral soil) in comparison to subalpine fir. This would be

reflected in subsequent stand development which would be more heavily influenced by subalpine fir and aspen than Engelmann spruce.

Disturbance interactions

Whether the antecedent fires were pre-dated by spruce beetle outbreak(s) is unknown; however, we suggest three reasons it is unlikely: 1) a lack of synchrony of fire dates between sites, in which all trees would have presumably been killed by an outbreak (i.e., similar stand conditions), 2) the presence of a large number of remnant spruce, which were not characteristic of the recent outbreak, and 3) we would expect remnant trees of non-host species to exhibit tree ring release in response to the canopy opening caused by a historic, pre-fire outbreak. Instead, although there were very minor releases e.g., Midway Point, Mammoth Creek, Navajo Lake, Rainbow Meadows, and Sydney Valley, remnant, non-host tree ring release on most of our sites rarely coincided with large amounts of initial rapid growth. Furthermore, recent modeling suggested extreme potential fire behavior is not an inevitable consequence of spruce beetle outbreaks (see Chapter 4).

Synchronized peaks of initial rapid establishment during the 1880s on Bristlecone Pine Trail, Midway Point, and Rainbow Meadows is coincident with the arrival of the first white settlers on the plateau who were primarily sheepherders. Early sheepherders have been noted to ‘set fire’ to the underbrush as they left the summer foraging grounds (Sampson 1923). It is possible these anthropogenic-caused range fires may have caused the more recent (post-1870s) peaks in tree establishment. These fires would burn at lower severities rarely becoming crown fires, and affect very small patches of forest adjacent to

the open meadows resulting in the release of some trees while leaving many remnants (e.g., Midway Point, Rainbow Meadows, Fig. 2.3). This is consistent with our observation that historic fires on the Markagunt Plateau have been of mixed severity, and that high-severity, stand-replacing fires are very infrequent and probably historically coincident with drought. Unfortunately, it was not possible to corroborate our fire dates with fire-scarred trees. The only fire-scarred individuals we found included one limber pine (reported in DeRose and Long 2007) that was not precisely dateable but had a ring count placing the fire scar in the 1880s, and a few fire-scarred Douglas-fir on Bristlecone Pine Trail and Navajo Lake that had characteristically rotten fire scars and were therefore not dateable. The lack of fire-scarred trees is expected given that the three primary subalpine species, Engelmann spruce, subalpine fir and aspen have extremely thin bark and are typically killed when exposed to fire.

Although the native Southern Paiute called the Markagunt Plateau ‘the smoking hills’ (Gregory 1949), it is unclear whether this was in reference to: 1) frequent understory fires characteristic of the lower elevation ponderosa pine forests (Battaglia and Shepperd 2007), 2) smoke as a result of geologically recent (ca 1000-5000 yrs ago) lava flows, or 3) fires in the high elevation spruce-fir forests. Furthermore, it is unknown to what extent natives had any influence on fire at high elevations. We suggest the Southern Paiute influence on fire in the spruce-fir forest was minimal. The snow-free season is short, June through October, and they likely avoided the area otherwise. During this short season fuel moisture is high, and summer monsoons occur almost daily between July 10th and the end of September (DeRose, unpublished data) making conditions to start and/or carry large

fires extremely rare. As a result it is unlikely Native American burning was responsible for our reconstructed antecedent disturbances.

Drought-mediated spruce-fir coexistence

Interactions between drought, fire, and spruce beetle outbreaks and their influence on the establishment of spruce-fir stands could not be decoupled; however, the affect of drought on stand development and regeneration has been demonstrated. It appears dryer conditions can be implicated: immediately prior to most of the antecedent fires, to the release of spruce and Douglas-fir during stand development (Table 2.4), and to patterns of understory regeneration of subalpine fir and aspen (Table 2.5). Therefore drought appears to be intimately connected with the occurrence of disturbances and, in the absence of large-scale disturbance, the drought cycle likely drives spruce-fir stand development.

Differential response of Engelmann spruce and subalpine fir to drought was indicated by species-specific patterns of tree ring release coincident with cyclical moisture conditions (Table 2.4). We suggest, in the absence of large-scale disturbance, cyclical drought drives spruce-fir coexistence. Differential tree mortality as a result of drought is not a new idea (see Mueller et al. 2005), and differential tree growth as a result of drought is also possible. It is likely the physiological mechanism controlling both of these phenomena is the relationship between leaf area index (LAI) and stand water relations. Available moisture (i.e., drought, Breda et al. 2006) largely controls the quantity of leaf area for a given stand and LAI is likely maintained at a dynamic equilibrium dictated by the long-term pattern of moisture deficit (Gholz et al. 1990). Furthermore, there are

species-specific differences in the contribution of individual-tree leaf area to stand LAI and, if each species' leaf area responds differently to drought, it would be reflected in their tree ring increment.

In response to decreasing moisture, stand LAI is reduced, coming disproportionately from some combination of needle, branch or stem death of the least drought-tolerant individuals, subalpine fir and possibly aspen. In contrast, Engelmann spruce shares tree ring release characteristics with drought-tolerant Douglas-fir, suggesting it is more drought-tolerant than subalpine fir. That subalpine fir is less drought-tolerant than Engelmann spruce has been previously demonstrated (Lopushinsky and Klock 1974, Knapp and Smith 1981); unfortunately, our data were not amenable to testing the hypothesis that subalpine fir died more often as a result of drought conditions. During periods of increasing moisture conditions Engelmann spruce, having better tolerated the drought (i.e., maintained a large crown) are better able to respond by increasing tree ring increment. Furthermore, Engelmann spruce has a structural advantage over subalpine fir because they are taller and tend to be canopy dominants, further enabling a more rapid response to periods of increasing moisture (Table 2.6). Where drought has this cyclical influence on stand development (i.e., Markagunt Plateau, Fig. 2.2) the maintenance of long-term canopy LAI about a dynamic equilibrium, given the disproportionate response of fir and spruce (Table 2.4), would tend to ultimately favor spruce and, in the absence of high-severity disturbance, result in spruce dominance. As an example, on our study sites stand age was highly correlated with pre-outbreak percent basal area (dominance) of Engelmann spruce ($r^2 = 0.647$, $P = 0.012$).

The relationship between stand LAI and water relations also explains the pattern of understory establishment with the drought cycle (Table 2.5). As LAI responds to increasing moisture conditions less soil water is available for potentially establishing advance regeneration, which is consistent with the observation that desiccation is likely the cause of seedling mortality in subalpine fir (Cui and Smith 1991), and with our observation that it is less likely to establish during increasing moisture conditions, coincident with tree ring release of spruce (Tables 2.4 and 2.5). Therefore, we argue that when canopy LAI is decreasing in response to drought conditions, because of the drop in water demand by canopy trees, more soil moisture is actually available for regenerating species (i.e., subalpine fir, Table 2.5).

Our proposed drought-driven model of spruce-fir coexistence is an extension of previously suggested models (Veblen 1986, Aplet et al. 1988). We add the direct consideration of climate because neither of these models address the climatic influence on stand dynamics but instead focus on the influence of disturbances. In pre-existing models life history traits were suggested as the mechanism for coexistence, i.e., long-lived spruce balanced fecund subalpine fir. This observation is not inconsistent with our model, where we speculate one reason spruce is more long-lived is because it is drought-tolerant, whereas one reason subalpine fir is shorter-lived is because it is likely drought-sensitive. However, treefall gaps, in the absence of large-scale disturbance, have been suggested to help mediate this life history balance (Veblen 1986) which assumes gaps are a common feature of the old-growth spruce-fir landscape and, although our stands on the Markagunt Plateau were very old (Table 2.1), the occurrence of gaps was very rare (Table 2.3).

CONCLUSIONS

In light of the recent (1990s), landscape-wide spruce beetle outbreak on the Markagunt Plateau, it was postulated that the antecedent disturbance might have been a previous beetle outbreak. However, multiple and consistent lines of evidence suggested mixed- and high-severity fire were the most likely antecedent disturbance. Furthermore, unlike the recent outbreak, the putative antecedent fires were spatially and temporally disparate in the period examined (1480-2000). Patterns of establishment and subsequent stand development were related to the regional drought cycle, which helped to explain putative fire events and species-specific differential growth rates. We suggest it is likely the disproportional growth response to drought ultimately led to homogenous spruce conditions and increased host susceptibility prior to the recent outbreak. Furthermore, we hypothesize that this differential response to cyclical drought/pluvial conditions is a possible mechanism of spruce-fir coexistence.

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TABLE 2.1. Site attributes for the study area.

Site	Average Elevation (m asl)	Aspect	Slope (%)	Age (years)	Site Index (m at base age 100)
Snotel	3202	North	5-45	492	24.1
Mammoth Creek	2670	North	15-40	491	16.2
Navajo Lake	2879	Northeast	10-30	470	25.9
Hancock Peak Trail	3081	Southeast	0-5	465	22.0
Bristlecone Pine Trail	3006	Northwest	15-40	437	22.8
Ashdown	3197	North	0-5	425	20.7
Lava Cone	2979	Variable	0-20	421	20.4
North Hancock	3090	North	3-30	323	18.9
Sydney Valley	3095	Southwest	3-15	309	22.5
Rainbow Meadow	3206	South	2-10	282	20.1
Midway Point	2959	North	0-3	276	24.9

TABLE 2.2. Pre-outbreak stand structural and compositional attributes by site for all trees > 5 cm DBH ordered by Engelmann spruce

quadratic mean diameter.

Site	Quadratic mean diameter		Relative basal area (as a percent)				No. plots
	All species	Engelmann spruce	Aspen	Engelmann spruce	Subalpine		
					fir	Other†	
Snotel	54.7	57.5	-	91.3	8.7	-	8
Ashdown	49.5	54.2	-	85.9	14.1	-	6
Rainbow Meadow	35.9	49.7	34.9	25.6	39.5	-	10
Hancock Peak Trail	41.9	48.5	1.9	74.8	23.4	-	10
Navajo Lake	47.6	46.8	0.4	55.5	19.5	24.7	20
Lava Cone	37.9	45.9	5.3	67.3	24.8	2.7	10
Bristlecone Pine Trail	52.6	43.0	-	68.3	8.0	23.3	8
Midway Point	36.3	41.4	24.1	65.2	10.8	-	10
Sydney Valley	28.6	39.3	32.8	18.0	48.4	0.8	10
North Hancock	33.2	37.1	-	72.4	27.6	-	10
Mammoth Creek	34.9	35.9	13.5	66.2	6.8	13.5	10

† Other includes in order of abundance: Douglas-fir, limber pine, ponderosa pine, blue spruce, white fir.

TABLE 2.3. Charcoal presence, pit and mound topography, and fuel loading for each site on the Markagunt Plateau.

Site	Charcoal [†] (%)	Pit (%)	Mound (%)	Fuel loading (Mg ha ⁻¹)	No. plots
Ashdown	40	0.04	0.43	131.2 ± 43.7	9
Bristlecone Pine Trail	50	0.03	1.10	136 ± 68	4
North Hancock	55	0.30	0.80	142.6 ± 45.1	10
Hancock Peak Trail	34	0.30	1.11	107.6 ± 34	10
Lava Cone	16	0.04	1.14	137.3 ± 43.4	10
Midway Point	48	0.28	1.41	143.1 ± 45.3	10
Mammoth Creek	35	0.03	1.04	93 ± 29.4	10
Navajo Lake	79	0.30	1.06	133.1 ± 42.1	10
Rainbow Meadow	18	0.21	0.97	128.2 ± 57.3	5
Snotel	66	0.31	0.03	158 ± 49.9	10
Sydney Valley	18	0.25	1.05	167.5 ± 52.9	10

Note: Pit and Mound are in percent measured on linear transects, fuel loading is all surface fuels including duff and litter.

[†] Percentage of plots with charcoal present.

TABLE 2.4. Results of Cochran-Mantel-Haenszel test for homogeneity of proportions showing Engelmann spruce and Douglas fir are at least twice as likely to release during increasing moisture conditions and aspen and subalpine fir are not different than chance †

Species	Odds ratio	Confidence Interval	P-value	No. sites
Engelmann spruce	2.001	1.504-2.67	<0.001	14
Douglas-fir	2.748	1.071-8.036	0.0037	2
Aspen	0.721	0.407-1.264	0.1427	5
Subalpine fir	1.343	0.942-1.92	0.0317	10

† Significance indicated by confidence intervals that do not include 1.0.

TABLE 2.5. Results of Cochran-Mantel-Haenszel test for homogeneity of proportions showing: spruce does not differ from chance, aspen is more likely to regenerate during peaks, and subalpine fir regenerates less than chance during troughs and increasing moisture and more than chance during decreasing moisture.†

Species	Odds ratio	Confidence Interval	P-value	No. sites
<i>-- peaks --</i>				
Engelmann spruce	0.785	0.242-2.198	0.705	10
Aspen	6.431	1.370-40.78	<0.001	11
Subalpine fir	0.837	0.587-1.188	0.185	5
<i>-- troughs --</i>				
Engelmann spruce	1.589	0.594-4.046	0.994	10
Aspen	0.326	0.028-1.952	0.147	11
Subalpine fir	0.633	0.441-0.904	<0.001	5
<i>-- increasing moisture --</i>				
Engelmann spruce	0.691	0.262-1.721	0.321	10
Aspen	0.693	0.166-2.646	0.482	11
Subalpine fir	0.605	0.437-0.835	<0.001	5
<i>-- decreasing moisture --</i>				
Engelmann spruce	1.447	0.581-3.813	0.321	10
Aspen	1.441	0.377-6.001	0.482	11
Subalpine fir	1.652	1.197-2.285	<0.001	5

† Significance indicated by confidence intervals that do not include 1.0.

TABLE 2.6. Mean height and crown ratio for canopy Engelmann spruce and subalpine fir on the study sites.

Site	Mean height (m)		Mean crown ratio [‡] (%)		No. spruce	No. fir
	Engelmann spruce	Subalpine fir	Engelmann spruce	Subalpine fir		
Ashdown	18.4	14.6	83	76	85	24
Bristlecone Pine Trail	23.5	16.8	78	84	22	5
North Hancock	19.9	14.6	75	72	62	28
Hancock Peak Trail	21.4	11.6	79	65	89	27
Lava Cone	22.5	15.5	71	82	77	35
Midway Point	20.9	17.0	70	63	104	28
Mammoth Creek	16.6	16.6	89	81	49	5
Navajo Lake	22.6	17.5	73	80	79	38
Rainbow Meadow	20.8	14.9	82	77	22	32
Snotel	22.7	12.0	74	75	105	12
Sydney Valley	21.2	16.6	77	70	23	70
	$P < 0.0001$ [†]		$P = 0.3301$ [†]			

[‡] Crown ratio is crown length / total tree height

[†] T-test for difference of means

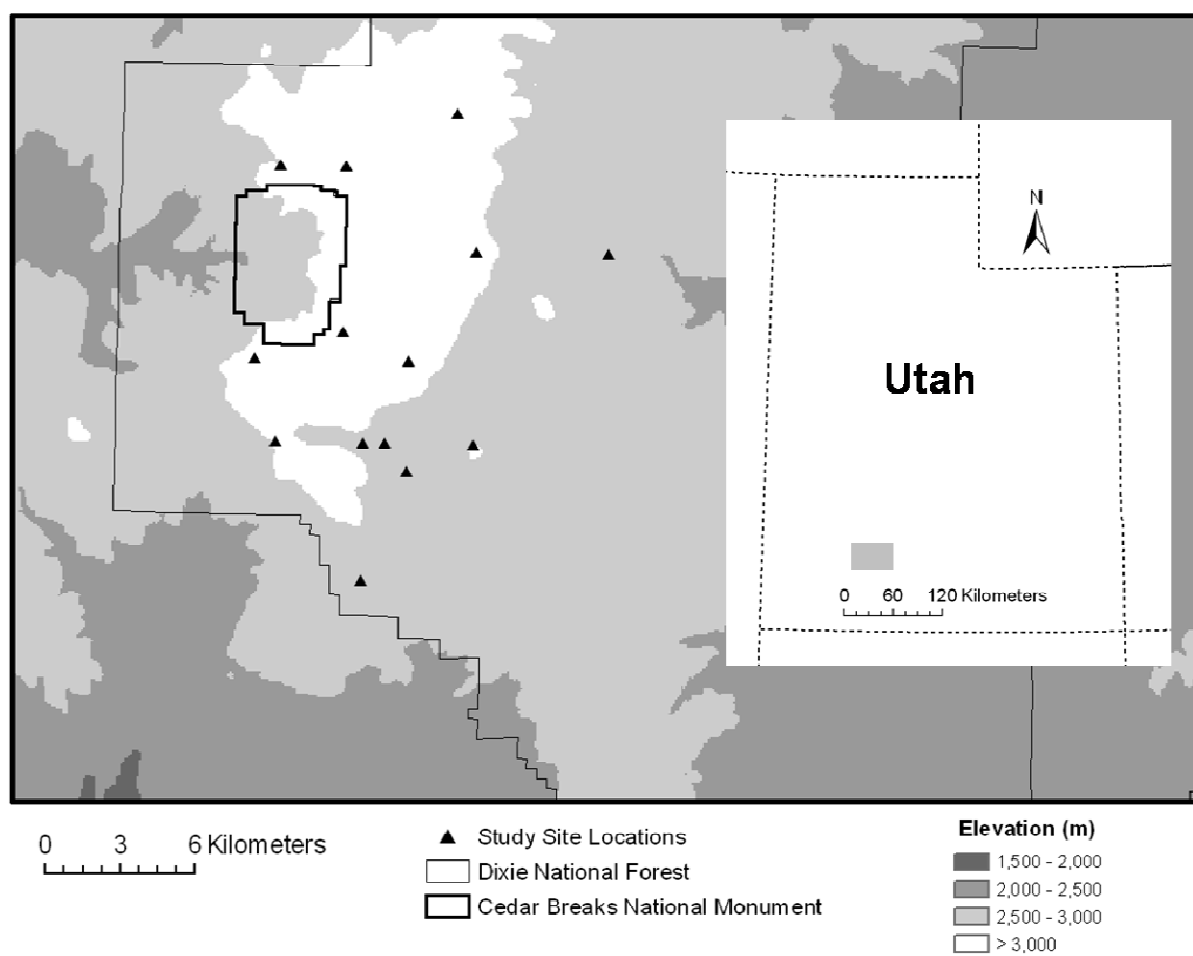


FIG. 2.1. Map of the Markagunt Plateau showing study locations.

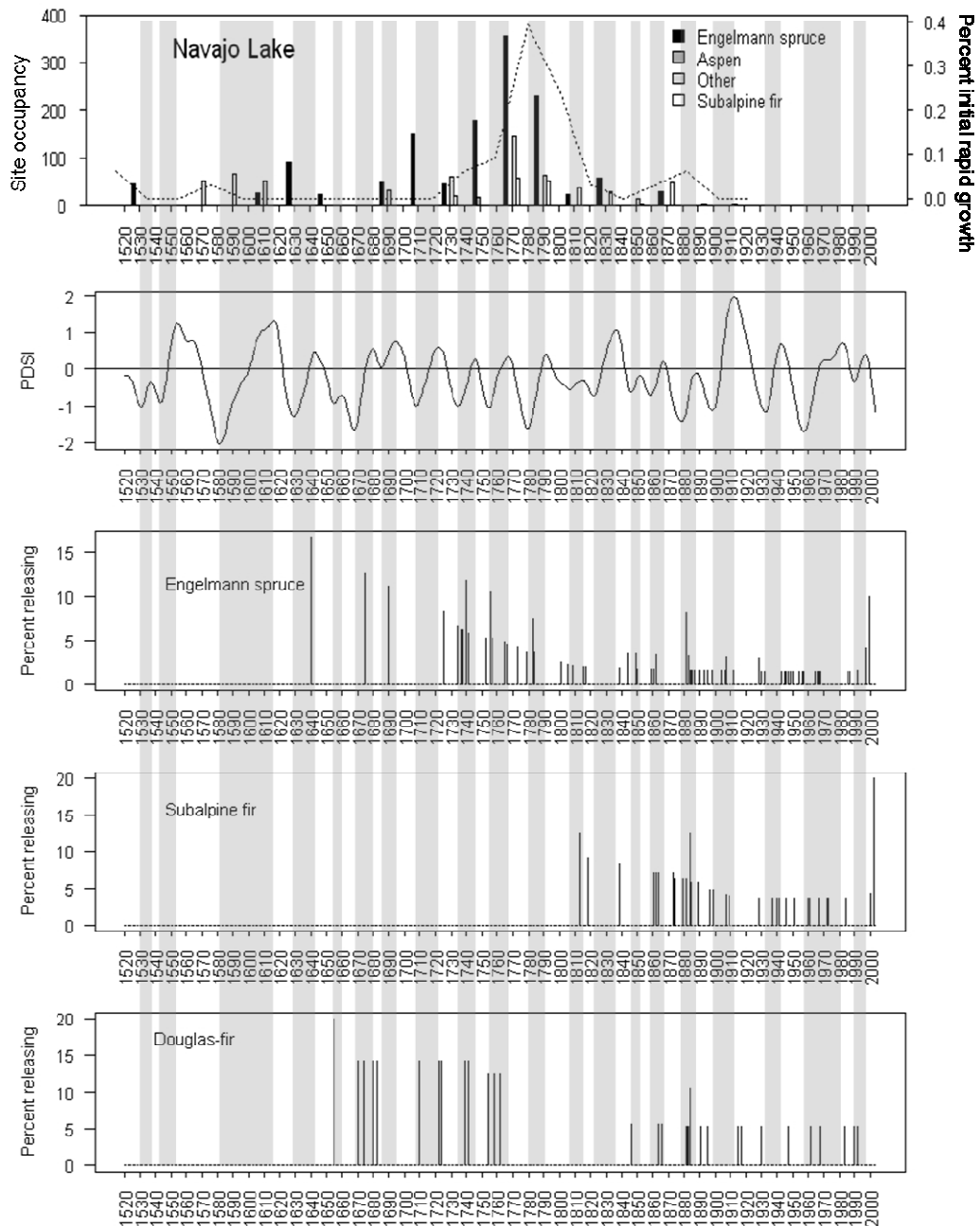


FIG. 2.2. Navajo Lake as an example of the graphical analyses performed for each site which shows the occurrence of Palmer Drought Severity Index with overstory site occupancy and tree ring release by species. Grey area indicates areas of increasing moisture conditions, white areas decreasing moisture. Abscissa scale is the same for each panel.

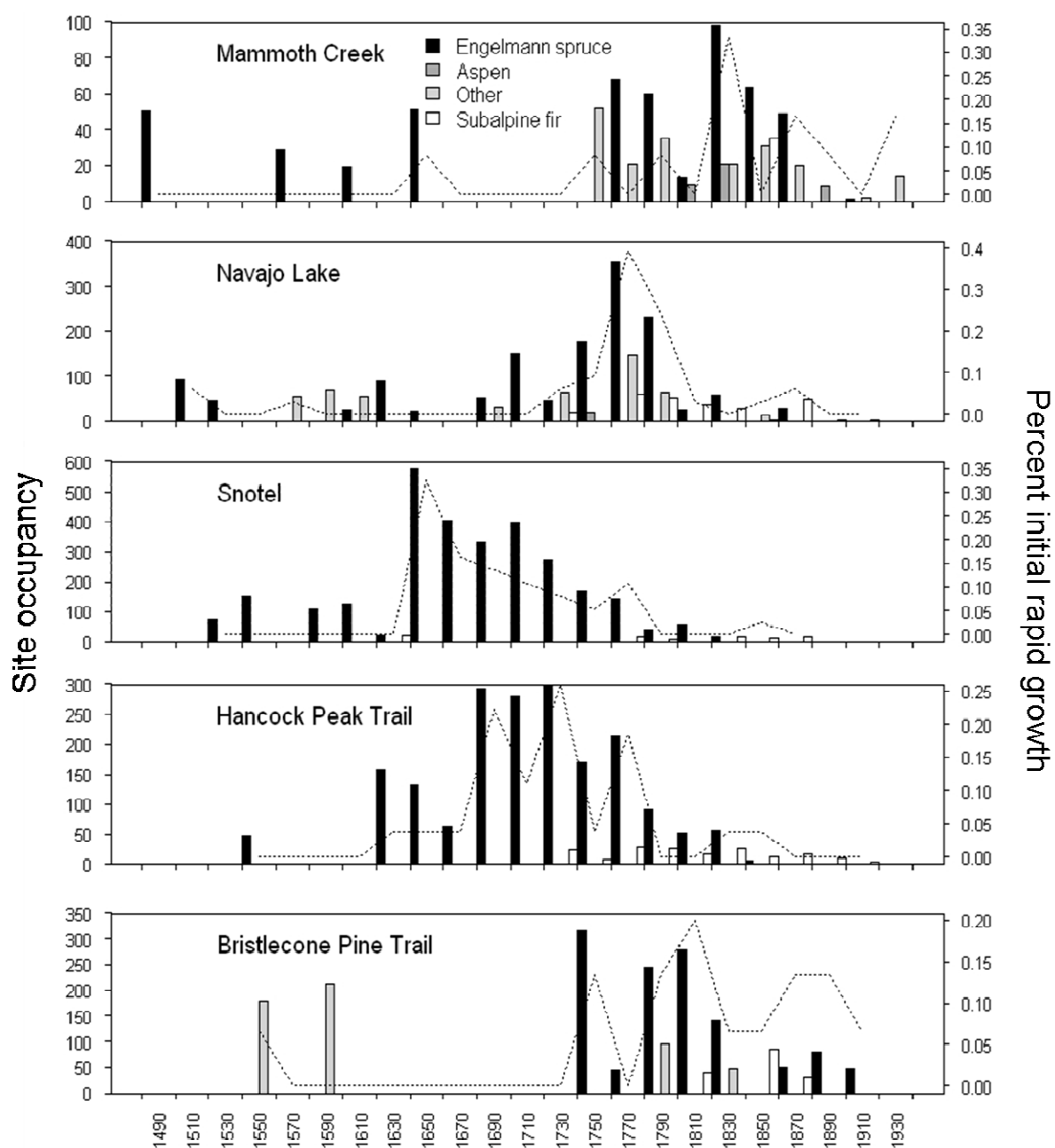


FIG. 2.3. Age structures with initial rapid establishment juxtaposed for all sites. Note primary and secondary ordinate scales differ by site, abscissa scale is identical. Sites ordered by stand age (Table 1).

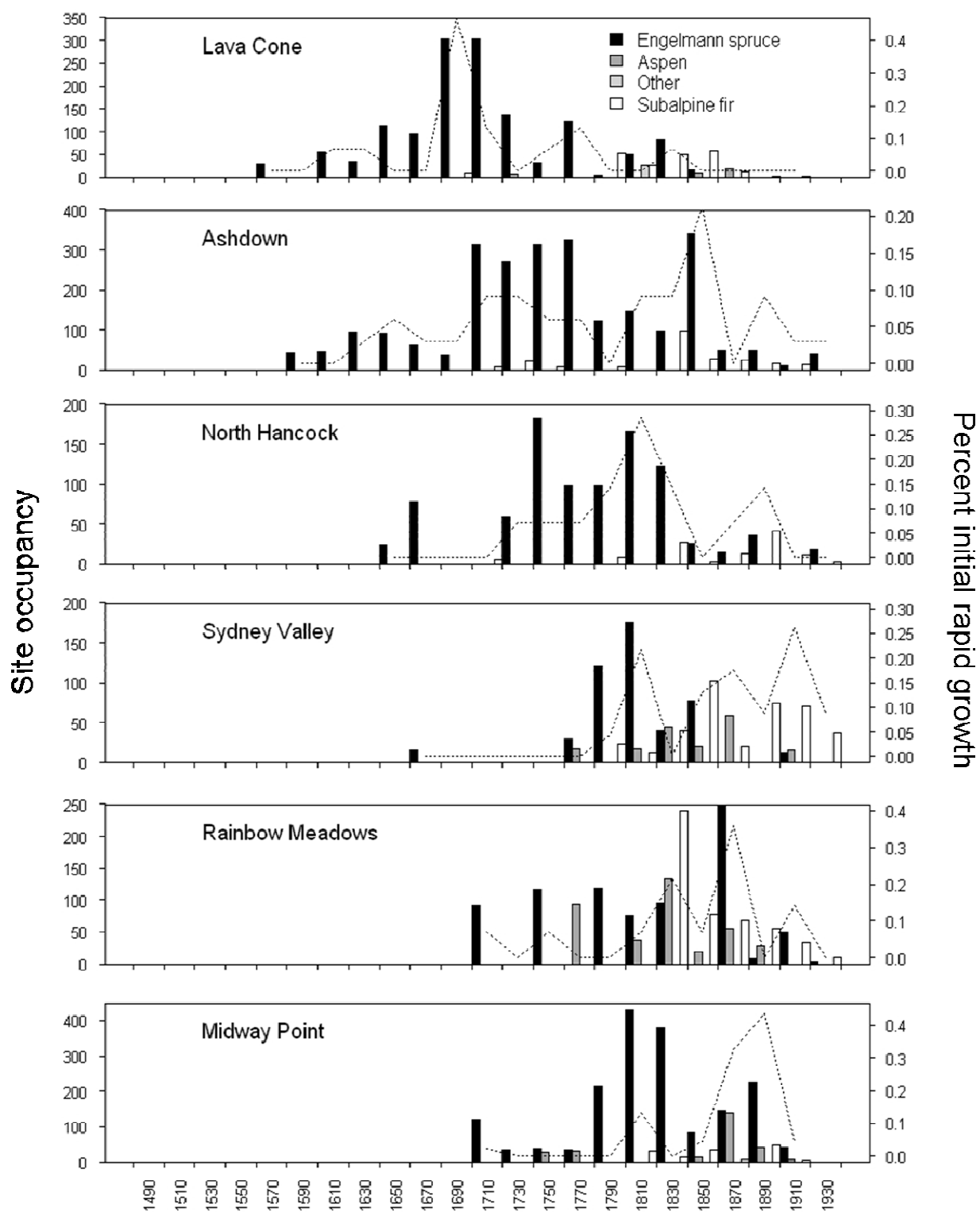
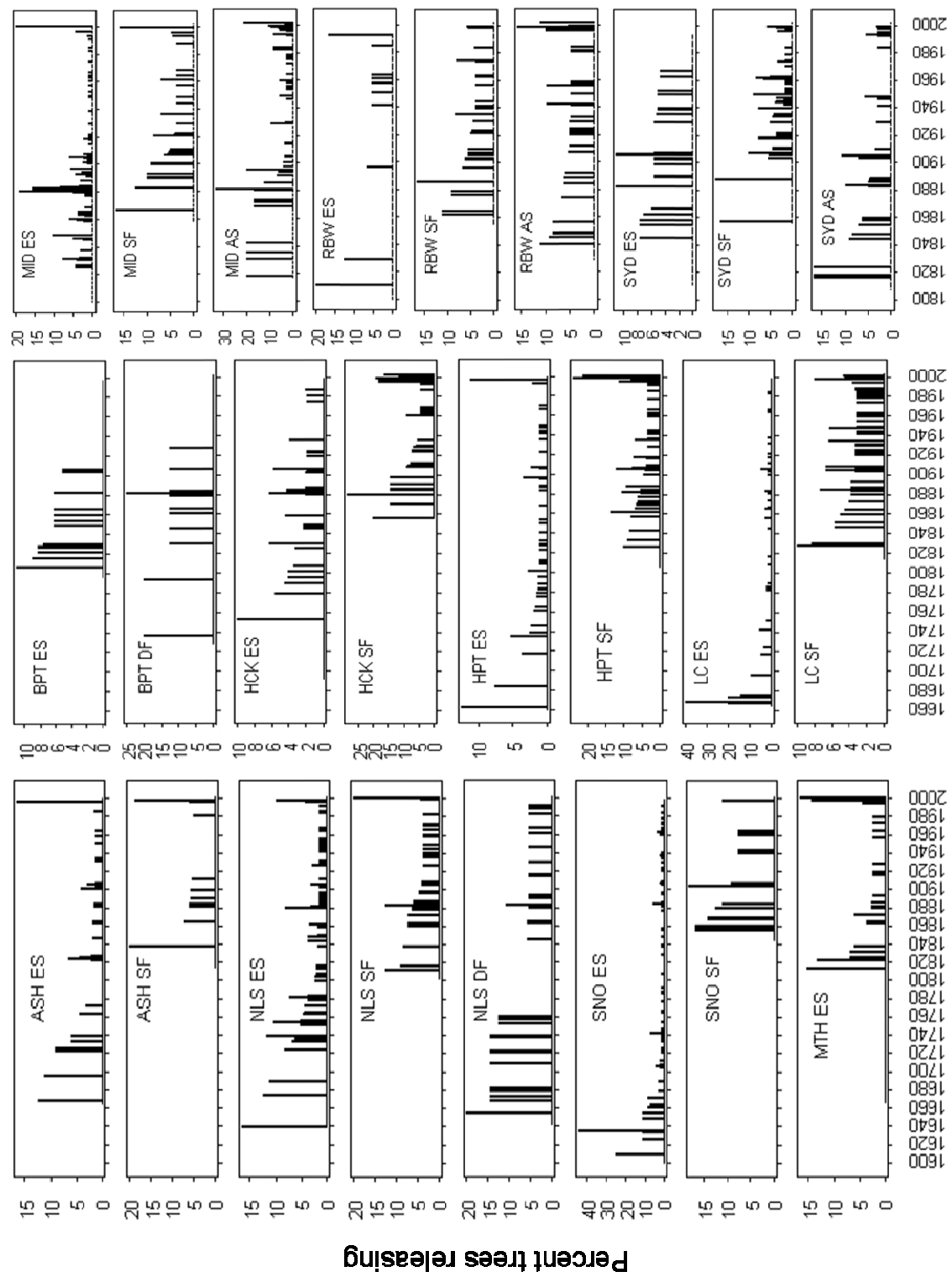


FIG. 2.3 cont.

FIG. 2.4. Percent of trees releasing for each species at each site with > 5 trees in the chronology. Release criteria was 100% increase in ring width for 5 year groups. Note differing scale for ordinate axes and similar abscissa scale for each column. ASH – Ashdown, ES – Engelmann spruce, SF – subalpine fir, NLS – Navajo Lake, DF – Douglas-fir, SNO – Snotel, MTH – Mammoth Creek, BPT – Bristlecone Pine Trail, HCK – North Hancock, HPT – Hancock Peak Trail, LC – Lava Cone, MID – Midway, AS – aspen, RBW – Rainbow Meadows, SYD – Sydney Valley.



CHAPTER 3

ANATOMY OF A SPRUCE BEETLE OUTBREAK: RECONSTRUCTION OF
SPATIOTEMPORAL DYNAMICS ³**Abstract**

Spruce beetle outbreaks are important drivers of ecosystem dynamics in spruce-fir forests. Unfortunately the spatiotemporal dynamics of possible outbreak patterns are not well-understood. A landscape-wide spruce beetle outbreak (late 1980s-1990s) on the Markagunt Plateau, southwestern Utah resulted in the mortality of virtually all the Engelmann spruce. The recent outbreak provided an excellent opportunity to investigate, quantify, and further understand outbreak spatiotemporal dynamics. A multi-level approach to analyze spatiotemporal outbreak dynamics using spatial point data and dendrochronological techniques was undertaken. Engelmann spruce mortality attributed to the spruce beetle was used as a proxy for spruce beetle population levels during the course of the outbreak. At the landscape extent, moist sites with large Engelmann spruce were where beetle populations transitioned from the endemic-to-epidemic phase. Within stands, old, large spruce in relatively pure stands succumbed earlier to the beetle. As the outbreak evolved over time, temperature anomalies accelerated beetle population growth leading to a reduction in the time it took for all spruce on a given plot to be killed. Although independent, building beetle populations were relatively spatially synchronous and the timing of eruption on the landscape was influenced by host and environmental conditions.

³ Coauthored by R. Justin DeRose and James N. Long

Introduction

Spruce beetles (*Dendroctonus rufipennis* Kirby) are a pervasive natural disturbance process in Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) forests of western North America where they may be as important as stand-replacing fire in shaping these forests (Veblen et al. 1994). Many studies have documented the effects of spruce beetles on Engelmann spruce forests; however, despite their importance in structuring spruce-fir systems, little or no work exists that describes the details of spatiotemporal dynamics of Engelmann spruce mortality over the course of an outbreak.

Three conditions are necessary for a spruce beetle outbreak to occur: (1) a populations of spruce beetles, (2) an appropriate range of temperatures, and (3) susceptible hosts (see Chapter 6). Once these conditions are met an inciting factor, typically thought to be wind thrown spruce (Schmid 1981), logging activities, or avalanches (Hebertson and Jenkins 2007), allows endemic beetle populations to build to epidemic levels. This is likely because as many as 10 times the number of beetles can be supported in prostrate stems compared to standing spruce (Nagel et al. 1957). To ensure the continuation of sufficient outbreak-level spruce beetle populations, thresholds associated with each condition must be maintained (Raffa et al. 2008). Pheromone-mediated mass attack can occur once the temperature threshold for daily flight is met (i.e., ~16° C Dyer 1973). After boring through the bark females deposit eggs in galleries constructed in the phloem. Larvae overwinter for one (univoltine) or two (semivoltine) years, completing four instars (a developmental stage of arthropods between each moult, until sexual maturity is reached) before emerging (Massey and Wygant 1954); however, extremely low winter temperatures can drastically reduce the survival of overwintering

larvae (Frye et al. 1974). If summer temperatures are unusually warm (Logan et al. 2003) (i.e., cumulative hours above 17 C elapsed from 40 – 90 days (Hansen et al. 2001)) a shift from mostly semivoltine to mostly univoltine beetle populations will result in accelerated spruce mortality (Hansen and Bentz 2003).

Susceptible host, the third condition for a beetle outbreak, is typically mature Engelmann spruce (>10 cm DBH) because the spruce beetle needs sufficiently large trees for successful brood production (Schmid and Frye 1977). However, individual trees are not sufficient to support epidemic populations; large and dense Engelmann spruce stands must be present on a large percentage of the landscape. Therefore, spruce beetle hazard ratings for spruce forests have traditionally characterized stands of large average tree diameter (> 40 cm mean diameter), with high densities (> 14 m² basal area), and a large percentage of spruce (> 65 %), as the most susceptible to beetle outbreaks (Schmid and Frye 1976). In addition, slower growing trees (radial increment) and those on dryer sites have been found to be more vulnerable to spruce beetle attack (Hard 1985, 1987). Reduced spruce radial increment may be associated with increasing stand density, climatic stress such as drought, or growth differences due to topographic differences (e.g., drier southwest versus moister northeast sites). Most often, attributes of susceptibility are used to describe the endemic-to-epidemic population building potential for particular spruce stands; however, attributes of susceptibility may also influence the spatial and temporal patterns of a spruce beetle outbreak.

Spatiotemporal patterns are a characteristic of any large-scale natural disturbance (Turner et al. 2001). For example, a large wildfire typically exhibits a wide range of behaviors within the fire perimeter that serve as useful analogies for insect outbreaks.

Large crown fires originating from a single ignition such as a lightning strike exhibit a ‘flame front’ that can spread rapidly across the landscape under severe weather conditions. In contrast, multiple spatially, and possibly temporally, disparate ignitions could create many smaller fires that would eventually coalesce, affecting most of the landscape resulting in different landscape structure. Some insect outbreaks may originate from an epicenter and spread across the landscape in a pattern best described as a traveling wave (Johnson et al. 2004), whereas other insect outbreaks may simultaneously arise in seemingly spatially independent areas (i.e., spatial synchrony) where populations build, and eventually coalesce (Okland and Bjornstad 2003). These straightforward descriptions of pattern assume homogeneous landscape conditions and host connectivity when natural conditions are usually actually heterogeneous. It is likely the heterogeneity in conditions on the landscape influences disturbance processes resulting in more complicated spatiotemporal patterns.

Beginning in the late 1980s, the largest and most severe spruce beetle outbreak ever recorded in Utah occurred on the Markagunt Plateau in the Dixie National Forest. The spruce beetle killed ~95% of the Engelmann spruce > 5 cm in diameter at breast height (DBH) over an area of at least 250 km² (DeRose and Long 2007). Virtually every beetle-killed spruce is still standing after the recent outbreak; therefore, we had the opportunity to reconstruct the pattern of Engelmann spruce mortality using dendrochronological techniques. In this paper we examined the spatial and temporal patterns of Engelmann spruce mortality during the Markagunt Plateau outbreak. We explored the influence of forest structure and composition and environmental variables, for individual trees, plots

and stands, on the spatiotemporal patterns of beetle-caused Engelmann spruce mortality across the landscape.

Methods

Study area

The Markagunt Plateau on the Dixie National Forest in southwestern Utah was chosen for analysis because the spruce beetle outbreak had recently killed virtually all the spruce on the plateau (Fig. 3.1). Regionally, the plateau is located on the western edge of the greater Colorado Plateau. Prior to the outbreak the high-elevation plateau was dominated by Engelmann spruce forests, which also commonly include subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), aspen (*Populus tremuloides* Michx.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), and limber pine (*Pinus flexilis* James). Precipitation on the plateau comes in two broad peaks a larger one in the form of winter snow from cold Pacific air and a smaller one during the summer as a result of the southwestern monsoon (Mock 1996). Long-term data from the Blowhard weather station (<http://climate.usurf.usu.edu/index.php>) showed mean annual precipitation for the period 1965 – 2005 was 739 mm (range 431 – 1202 mm) and for the same period minimum monthly temperature was -30.5 C and maximum monthly temperature was 32.2 C. Data from the Blowhard station were also used to analyze possible interactions between temperatures and beetle population levels based on known limitations to spruce beetle physiology (Dyer 1973, Hansen et al. 2001); specifically, whether annual summer (July, August, September) maximum, or winter (January, February, March) minimums influenced beetle populations.

Data collection

Stand selection on the plateau focused on areas that were homogeneous in overstory forest structure and showed no signs of human disturbance (i.e., logging). On intensively measured stands a number of plots were measured using a grid sampling approach with a random starting point and each plot was ~ 100 m apart. Extensive plots were located across the plateau in between the intensive plots in such a way as to characterize as much of the spruce forest as possible (Fig. 3.1).

Regardless of plot type (intensive or extensive) spatial data were collected with a global positioning sensor. Waypoints were recorded only when error was estimated to be < 3 m. Elevation, slope, and aspect were recorded for each plot. For each tree on the plot DBH and total height were measured and species and status (live or dead) were noted. For every dead spruce, the cause of death was noted, specifically whether or not it was killed by the spruce beetle recently (i.e., outbreak), or otherwise. The presence or absence of sloughing bark, beetle galleries, and beetle emergence holes were assessed in identifying the cause of death. Increment cores were taken near the base of the tree and coring spots were carefully selected where bark was persistent or where the smooth outer surface of the xylem was clear. Trees that were rotten or broken near the surface were avoided. Special care was taken when removing increment cores from the tree to maintain the integrity of the outermost rings for establishing DOD and to ensure multiple pieces were stored in their proper order. Cores were stored in paper straws and allowed to dry before preparation and analysis.

Increment core preparation

Increment cores from Engelmann spruce were prepared using standard dendrochronological techniques (Stokes and Smiley 1968) and were visually crossdated against a locally developed Englemann spruce master chronology. The locally developed chronology consisted of trees from a previously existing spruce chronology (K. Briffa and F.H. Schweingruber, World Data Center for Paleoclimatology Data Contribution, [sic] Ceader Breaks Engelmann spruce chronology, NOAA/NCDC Paleoclimatology Program, Boulder, Colorado, USA⁴) combined with increment cores collected opportunistically from any live spruce found on the plateau. Program COFECHA (Holmes 1983) was used to check dating of all tree ring series. After dating, the calendar year of the outermost ring was noted. These dates were assumed to be the years in which spruce beetle-caused mortality occurred. Individual-tree DOD from spruce determined to have been killed by the beetle should be strongly tied to spruce beetle populations because successful reproduction is contingent upon the death of the host (Hopkins 1909).

Spruce beetle activity

The dependent variable, chosen to describe spruce beetle activity during the spruce beetle outbreak, was crossdated Engelmann spruce DOD. A large suite of stand and plot descriptors of forest structural and compositional attributes were calculated from the tree data for use as independent variables. To characterize older spruce plots, plot quadratic mean diameter (QMD) was calculated. To characterize the composition of spruce on a plot-by-plot basis, the percentage of Engelmann spruce stand density index (%SDI), was

⁴ URL: <http://www.ncdc.noaa.gov/paleo/treering.html>

calculated for plots using the summation method (Shaw 2000). To characterize the overall density of the stand, SDI was also calculated using the summation method and averaged over the plots within the site. To characterize site potential productivity site index (SI) was calculated for stands using the heights and ages of 10 dominant trees in each stand (Alexander 1967). In addition, elevation and aspect, and individual-tree DBH were also used as independent variables (Table 1). A linear value of aspect that ranges from 0 – 1.0 was calculated, aspect value (AV), and is interpreted as 0 = drier southwesterly aspects to 1.0 = moist northeasterly aspects (Roberts and Cooper 1989).

Data analysis

To take full advantage of the data, analyses were conducted at two different extents: stand and landscape. Stand analysis of spruce beetle pattern was done using individual trees within plots within stands from intensive plots only (Table 3.1). No extensive plots were used because they had no within-plot variation in DOD years. The dependent variable in this analysis was the individual spruce DOD relative to the first year of beetle activity (rDOD) for the respective stand, so that if the first beetle-killed tree was in 1990, rDOD = 0, 1991, rDOD=1, 1992, rDOD = 3 etc. Because ecological processes such as spruce beetle outbreaks are inherently spatiotemporally correlated, standardizing to rDOD allowed the stand-by-stand outbreak dynamics to be evaluated independent of spatial and temporal patterns on the landscape. That is, regardless of when or where beetle populations first started building in the stand, what influenced their activity during the outbreak?

Landscape analysis of spruce beetle pattern was done using the first year of Engelmann spruce mortality for each plot within the landscape (Fig. 3.1) as the dependent variable because it is an indicator of when the first spruce beetle activity occurred on the plot. Two types of data were used for this analysis intensively and extensively measured plots (Table 3.1). Intensive plots are part of a larger stand and DOD was determined for all the Engelmann spruce on the plot. On extensive plots DOD were determined for one or two spruce and the earlier of these was assumed to be the first year of beetle attack. Finally, modeled patterns of rDOD stand-by-stand that complemented the analysis of the first year of beetle activity plot-by-plot on the landscape were further examined in order to reconcile the two analysis extents.

For both analyses generalized linear models were used with a suite of independent variables and evaluated based on their deviance (D^2 , or pseudo R^2). Previous studies have suggested possible risks when analyzing spatiotemporal data with linear models because of the possibility that observations might not be independent (Aukema et al. 2008). While a lack of independence imposes limitations for predictive modeling, this assumption should not necessarily restrict explanatory analysis of ecological processes which are inherently spatiotemporal. Nevertheless, standardizing the dependent variable in the stand analysis rendered the data independent, both in space and time. For the landscape analysis we used non-standardized values and explicitly acknowledged the possibility that the observations might not be independent in order to potentially gain further insight into spruce beetle outbreak dynamics.

Results

As an indicator of beetle populations, crossdated tree rings indicated individual Engelmann spruce were killed by the beetle from 1987 through 2007. The timing of the year of first beetle activity on the plots ranged between 1987 and 2001 (Table 3.2). Over this ~20 yr period the spruce beetle outbreak killed virtually all the spruce on the landscape (> 95%, DeRose and Long 2007). The spatiotemporal pattern of spruce mortality across the Markagunt Plateau was complex (Fig. 3.1) and was influenced by stand and landscape characteristics that suggested the outbreak did not simply spread in traveling waves like an idealized wildfire ‘flame front’. Instead, a more complicated pattern of spatial synchrony emerged where multiple, individual foci of building beetle populations across the landscape eventually coalesced.

Stand patterns

Standardization of DOD on a stand-by-stand basis allowed us to evaluate each stand independently and showed that, within a particular stand, beetle-killed trees were not related in space or time, rather, Engelmann spruce DOD on a tree-by-tree basis, was influenced by site potential productivity, stand structure, and environmental attributes. Within each of our 14 stands: (1) large diameter spruce were killed earlier than smaller spruce, (2) trees on plots with higher than average spruce size were killed earlier than those from plots with smaller average spruce, (3) individual trees in stands with high density overall were killed earlier than those from lower density stands, (4) individual trees on less potentially productive sites were attacked earlier than those from more potentially productive sites, and (5) individual trees on southwesterly plots (i.e., drier),

within the stand, were killed earlier than those from more northeasterly plots (i.e., moister) (Table 3.3). For example, within the Ashdown stand DOD showed no spatiotemporal pattern (data not shown); however, there was a negative relationship between DOD and diameter (Fig. 3.2). Although the stand model was variable ($D^2 = 0.34$), it indicated that, independent of what happened on the landscape, within a given stand, spruce beetles attacked and killed larger spruce that occur on old, dense, and dry plots first.

Landscape patterns

The pattern in timing of the first year of beetle-killed Engelmann spruce across the plateau (Fig. 3.1) was influenced by forest composition and environmental attributes and reflected the large variation in the data ($D^2 = 0.41$). Model error terms were autocorrelated (Breusch-Godfrey test, $P = 0.089$); however, bias was not apparent over latitude or longitude. This suggested autocorrelation was temporal, exactly what we would expect of an eruptive insect, given the stand results and the spatial synchrony of building populations. Interpretation is therefore temporal not spatial, i.e., when the beetle began building, not where. In general across the landscape, moist plots with higher spruce density were where spruce beetle populations built first. Specifically, Engelmann spruce on plots with a higher percentage of spruce composition were killed earlier than on plots with lower percentages (Table 3.4). Similarly, spruce on higher elevation plots with northeasterly aspects were killed earlier than those from lower elevations and southwesterly aspects (Table 3.4). In addition, the significant positive interaction between

elevation and aspect suggested spruce forest killed by the beetle was more predominate at higher elevations and northeasterly aspects (Table 3.4).

Reconciling stand and landscape patterns

Similarities in stand and landscape susceptibility to spruce beetle activity (i.e., spruce homogeneity) in combination with seemingly disparate results (i.e., influence of aspect at different scales) must be reconciled to understand the spatiotemporal outbreak pattern. Plotting the residual variation (standard deviation) from the stand model (Table 3.3) over the first year spruce beetle-killed Engelmann spruce occurred for all plots on the plateau revealed a strong negative linear relationship (Fig. 3.3). This suggested the landscape pattern of spruce beetle activity was superimposed upon the stand pattern, and that they were not mutually exclusive. As the outbreak built on the landscape, the rate of individual-tree mortality within a given plot decreased over time (Fig. 3.3).

The combined effect of multi-scale spatiotemporal patterns of spruce beetle outbreaks suggested multiple, seemingly independent beetle population foci were building across the landscape. These multiple foci continued to build and spread locally, influenced by individual-tree attributes (Table 3.3), but occurred across the landscape in response to specific landscape attributes (Table 3.4) and appeared as multiple, outbreak epicenters that eventually coalesced. The spatial synchrony of seemingly independent outbreak epicenters across the plateau suggested an overriding environmental factor incited the beetle populations to build. Indeed, increased summer maximum (~1995-2003) and winter minimum temperatures (~1991-2000) appeared to coincide with endemic to

epidemic beetle population shifts and resultant large-scale spruce mortality across the Markagunt Plateau (Fig. 3.4).

Discussion

Reconstructed spatiotemporal patterns of the spruce beetle outbreak on the Markagunt Plateau did not simply behave like the ‘flame front’ of large crown fires, spreading from a single ignition across the landscape in traveling waves. Nor did it solely exhibit spatial synchrony in multiple, independent ‘ignitions’ of building beetle populations that coalesce over time. Rather, relatively synchronous (1987 – 1993) eruptions of building beetle populations occurred in spatial independent regions predictably over time on the larger landscape. That is, there was predictable spatial and temporal pattern, on the landscape, to the relative synchrony in spatially and temporally disparate erupting beetle populations. Like a wildfire complex, with multiple ignition sources in areas of higher susceptibility (i.e., higher flammability), the beetle outbreak erupted in moist, high elevation areas that had large Engelmann spruce. Under severe fire weather, the wildfire complex first spreads to areas of higher flammability through ‘spot fires’, skipping areas of lower flammability (‘hold-outs’), before finally coalescing. In a similar way the beetle outbreak evolved under ‘extreme temperature anomalies’, developing in highly susceptible areas, (‘spots’ on the landscape, and leaving areas of low susceptibility (‘hold-outs’, before moving into less susceptible areas. Given the continued presence of temperature extremes, areas of least susceptibility (hold-outs) were attacked and the outbreak coalesced.

The distribution of beetle-killed trees over time (Fig. 3.4) served as a template for the evolution of beetle populations over the course of the outbreak. As the outbreak progressed from endemic (~1987 – 1989) to building (~1990 – 1993) through epidemic (~1994 – 2002) population phases and finally collapsed (~2003), spatiotemporal patterns of spruce mortality were found to be related to forest structure and composition, environmental conditions, and overriding temperature anomalies. Results and interpretation from our analysis of spatial point pattern as the dependent variables in this study were not inconsistent with results from other studies where spatiotemporal pattern was described using patches.

What happened on the Markagunt Plateau?

Endemic phase

It is widely thought that the spruce beetle outbreak began on or near Brian Head or Sydney Valley, possibly in logging slash, during the early 1990s (Steve Munson, Matt Hanson, personal communication), which is partially consistent with our data (+ in Fig. 3.1). However, spruce beetle populations that occurred as early as 1987 – 1989 were also apparent in other stands across the plateau (i.e., Ashdown, North Hancock, Navajo Lake, Snotel in Fig. 3.1) although tree mortality was low (Fig. 3.4), suggesting endemic beetle populations were prevalent across the plateau likely reproducing in large, mature spruce.

Building phase

From 1990 – 1992 the number of beetle-killed trees started to grow indicating building beetle populations (Fig. 3.4). The development of the outbreak on the landscape appears not simply as spread from existing adjacent populations, but as multiple,

seemingly independent beetle population foci (e.g., Bristlecone Pine Trail, Lava Cone, Hancock Peak Trail, Midway Point, Mammoth Creek in Fig. 3.1), evidence for spatial synchrony (Okland et al. 2005). However, it is unknown whether the building beetle populations were truly independent or influenced by immigration from other populations, as has been found for building mountain pine beetle populations (Aukema et al. 2006). This would be impossible to measure unless individual beetles were monitored. It is likely not a coincidence that the amelioration of winter minimum temperatures, which should check overwintering beetle populations from time to time (Frye et al. 1974), began during this period (~ 1991) (Fig. 3.4). We suggest this anomaly was likely a catalyst for the endemic-to-building population phase shift. Building populations found adequate host because the Engelmann spruce stands on the Markagunt Plateau are many centuries old (see Chapter 6) and therefore these communities have been susceptible, i.e., had high hazard for a long time. Therefore, although susceptible host was historically present, beetle populations did not begin to build until incited by climate.

Once incited, the landscape model suggested plots with high spruce relative density, higher in elevation, and on more northerly aspects had beetle-killed trees earlier during the outbreak. Similarly, the stand model suggested trees in older, spruce-dominated plots with a high percentage of spruce in the stand were killed earlier during the outbreak. This is generally consistent with the spruce beetle hazard rating (Schmid and Frye 1976). However, in contrast to Schmid and Frye (1976), trees that occurred on sites of lower potential productivity were killed earlier than those on sites of high potential productivity. This inconsistency is attributed to the observation that, at least initially during an outbreak, spruce beetles preferentially attack more stressed (lower radial

increment) trees, which is more likely to occur on less productive sites. In general the stand and landscape results were consistent. One notable exception was the effect of aspect, which was negatively related to DOD when assessed on the landscape but positively related when assessed stand-by-stand. This seemingly contradictory result has an ecologically important explanation. On the landscape, moist, spruce-dominated plots are where beetle populations are more likely to ‘arrive’ (or build from endemic); as a result, plots on northeasterly aspects were more likely to have spruce beetle activity earlier in the outbreak (Table 3.4). However, in individual stands, once beetle populations had ‘arrived’ and begun to build, they were more likely to attack stressed trees, probably more common on southwesterly aspects (Table 3.3).

Epidemic phase

The spatial synchrony of building beetle populations occurred during a relatively short time period (1987-1993), after which they transitioned to epidemic levels rapidly (~1995) that continued until ~2003 (Fig. 3.4). During this period beetle populations exerted a large influence on the landscape, appearing on extensive plots but also killing spruce on previously uninhabited plots within stands (e.g., Ashdown, Bristlecone Pine Trail, North Hancock, Midway Point, Lava Flow in Fig. 3.1) since they take over a decade to kill all the trees in a given stand (Table 3.2). In addition to the amelioration of winter minimum temperature, which continued through ~2001, an unprecedented increase in summer maximum temperature began ~1995. We suggest that this unusually warm anomaly likely triggered a switch from semivoltine to univoltine beetle populations that accelerated spruce beetle population growth (Fig. 3.4). Only after the shift in these

two climatic anomalies was the full-blown epidemic evident (Fig. 3.4). This is not the first study to find temperature anomalies prior to and coincident with bark beetle outbreaks. Changes in climate have been cited as contributing factors to unprecedented outbreaks of both the spruce beetle (Berg et al. 2006), and the ongoing mountain pine beetle outbreak in British Columbia (Aukema et al. 2006). Temperature changes on the Markagunt Plateau are peculiar because the timing of the anomalies differs by many years. That observed beetle population dynamics could be explained by considering both temperature anomalies further suggests they are more likely responsible for the landscape-wide synchronous signal in building populations as opposed to more local triggers such as logging and wind throw, or to rapid spread as a result of host connectivity (Okland et al. 2005).

Once at epidemic levels, mass-attacking spruce beetle populations were likely less demanding about host conditions. For example, beetles may kill spruce in a given area faster than they would at endemic population levels, or attack marginally suitable small trees, or possibly attack the rare individual spruce present in other forest types (e.g., mixed-conifer) because it is the only remaining host substrate on the landscape. The decrease in plot variability in DOD over time (Fig. 3.3), in combination with the temporal distribution of spruce beetle-killed trees (Fig. 3.1), strongly suggests that, as the outbreak progressed, beetle population pressure rapidly intensified and accelerated spruce mortality. Therefore, spruce on plots attacked later during in the outbreak more rapidly succumbed to exacerbated beetle populations than those attacked earlier (Fig. 3.3). The incredible beetle pressure might also explain why they attacked such small trees (as small

as 6.5 cm DBH, unpublished data, this study), and relatively rare Engelmann spruce in other forest types (< 7% spruce composition, Table 3.1).

Outbreak collapse

Finally, from ~2000-2003 Engelmann spruce mortality plummeted rapidly, suggesting spruce beetle populations did as well, likely due to a lack of suitable host, although the drop in population also coincided with a return to normal temperature regimes (Fig. 3.4), which was almost certainly coincidental. Spruce mortality became rare after ~2003 and occurred primarily in remote stands and in drainages at the fringe of the spruce-fir zone, presumably because these were the only remaining live spruce on the landscape.

Other considerations

Challenges and opportunities were encountered in the modeling approach due to the use of spatial point data as dependent variables. Previous studies of bark beetle spatiotemporal dynamics have been conducted assuming beetle-caused mortality occurred as ‘patches’ (i.e., pixels) (Powers et al. 1999, Aukema et al. 2006). Regardless, there were similarities between our results from spatial points and those from other studies using generalized pixels. The patch approach, while yielding important insights into disturbance dynamics, can not assess the considerable variability within patches. For example, if we had analyzed each of our intensive stands as patches of spruce beetle mortality we would have necessarily ignored variation in DOD of more than a decade (Table 3.2). Similarly, when identification of beetle-killed patches is done by visual examination of the transition from green to grey attack stages there is necessarily ~ 1 – 3

yrs of variation regarding actual DOD due to the time it takes the foliage on a beetle-killed tree to turn from green to yellowish-green to grey (Schmid and Frye 1977). In contrast, crossdating to determining DOD can more precisely characterize the timing of tree death, the precise cause of tree death, and the spatial point pattern of tree death; however, precise determination of DOD does have limitations.

For example, inferring DOD from the outermost ring has been shown to vary by up to three years (Mast and Veblen 1994). Also, measuring individual trees across the landscape is incredibly time consuming compared to remote sensing of patches, and therefore data precision comes at the expense of characterizing the extent of an outbreak. This limitation was partially addressed by measuring both intensive plots as parts of larger stands across the plateau, and then ‘filling in’ with extensive plots of less measurement intensity to try and capture spatial variation across the landscape.

Summary and conclusions

The analysis of pattern using spatial points in this study provided a unique look at the anatomy of a spruce beetle outbreak by revealing novel insight into spatiotemporal dynamics. Results and interpretation of spatiotemporal pattern were strikingly similar to recent studies of other eruptive bark beetle species. In contrast to the common perception that spruce beetle outbreaks ‘move or spread’ across the landscape, we found spatial synchrony of multiple, building populations characterized the Markagunt Plateau outbreak. The variation in predictions of DOD suggest that, while the heterogeneity of host conditions on the landscape and temperature anomalies both potentially influenced spruce beetle populations, there are likely other factors that contributed to the observed

spatiotemporal patterns. Future studies that combine the data precision of dendrochronological approaches with the characterization of landscapes using appropriately sized pixels could further the understanding of bark beetle outbreaks.

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Table 3.1. Attributes of independent variables for the stand and landscape models

Analysis	Variable	Level	Mean \pm Standard deviation	Range	Sample size
Trees within stands	Diameter at breast height	Tree	46.3 \pm 16.4	6.5 – 106.5	637
	Plot quadratic mean diameter of Engelmann spruce	Plot	46.7 \pm 10.4	23.3 – 71.7	102
	Stand density index	Site	905 \pm 146	507 – 1159	14
	Site index	Site	22.1 \pm 2.65	16.2 – 25.9	14
	Aspect Value	Plot	0.68 \pm 0.33	0 – 1.0	102
Plots within landscape	Aspect Value	Plot	0.64 \pm 0.35	0 – 1.0	131
	Elevation	Plot	3004 \pm 163	2619 – 3338	131
	Percentage of Engelmann spruce stand density index	Plot	0.58 \pm 0.26	0.07 – 1.0	131

Table 3.2. Median \pm standard deviation, range and sample size for individual spruce date of death in intensively sampled stands and extensively sampled plots.

	Number on Fig. 1	Median	\pm	Standard deviation	Range	Sample size
Intensive stands						
Ashdown	1	1996	\pm	2.2795	1988 - 2000	66
Bristlecone Pine Trail	2	1999	\pm	3.1355	1991 - 2005	20
North Hancock	3	1996	\pm	2.3246	1987 - 2001	49
Hancock Peak Trail	4	1998	\pm	2.2239	1990 - 2004	76
Lava Cone	5	1997	\pm	2.3425	1990 - 2002	61
Lava Flow	6	1997	\pm	2.1368	1991 - 2001	17
Midway Face	7	1999	\pm	2.8284	1991 - 2002	15
Midway Point	8	2000	\pm	2.4624	1991 - 2006	94
Mammoth Creek	9	1998	\pm	3.2593	1991 - 2007	39
Navajo Lake	10	2000	\pm	2.8781	1987 - 2006	60
Rainbow Meadows	11	1996	\pm	1.088	1994 - 1998	17
South Face	12	2000	\pm	0.301	1999 - 2000	11
Snotel	13	1997	\pm	2.7789	1988 - 2006	93
Sydney Valley	14	1996	\pm	1.5082	1994 - 2001	19
Extensive plots	-	1998	\pm	3.082	1989 - 2005	32

Table 3.3. Results of individual tree within stands analysis of timing of beetle attack

Variable	Estimate	Standard error	T-value	P-value
Intercept	0.162	1.103	0.148	0.8827
Diameter at breast height	-0.026	0.0082	-3.179	0.001
Plot quadratic mean diameter	-0.038	0.0141	-2.685	0.007
Site stand density index	-0.0049	0.00088	-5.670	<0.0001
Site index	0.563	0.0496	11.344	<0.0001
Aspect value	3.971	0.3918	10.135	<0.0001

Table 3.4. Results of landscape analysis of timing of initial beetle attack

Variable	Estimate	Standard error	T-value	P-value
Intercept	2073	13.07	158.5	<0.0001
Aspect Value	-63.05	15.80	-3.99	<0.0001
Elevation	-0.024	0.004	-5.689	<0.0001
Percent Engelmann spruce stand density index	-3.965	0.989	-4.006	<0.0001
Aspect value X elevation	0.020	0.0052	3.833	<0.0001

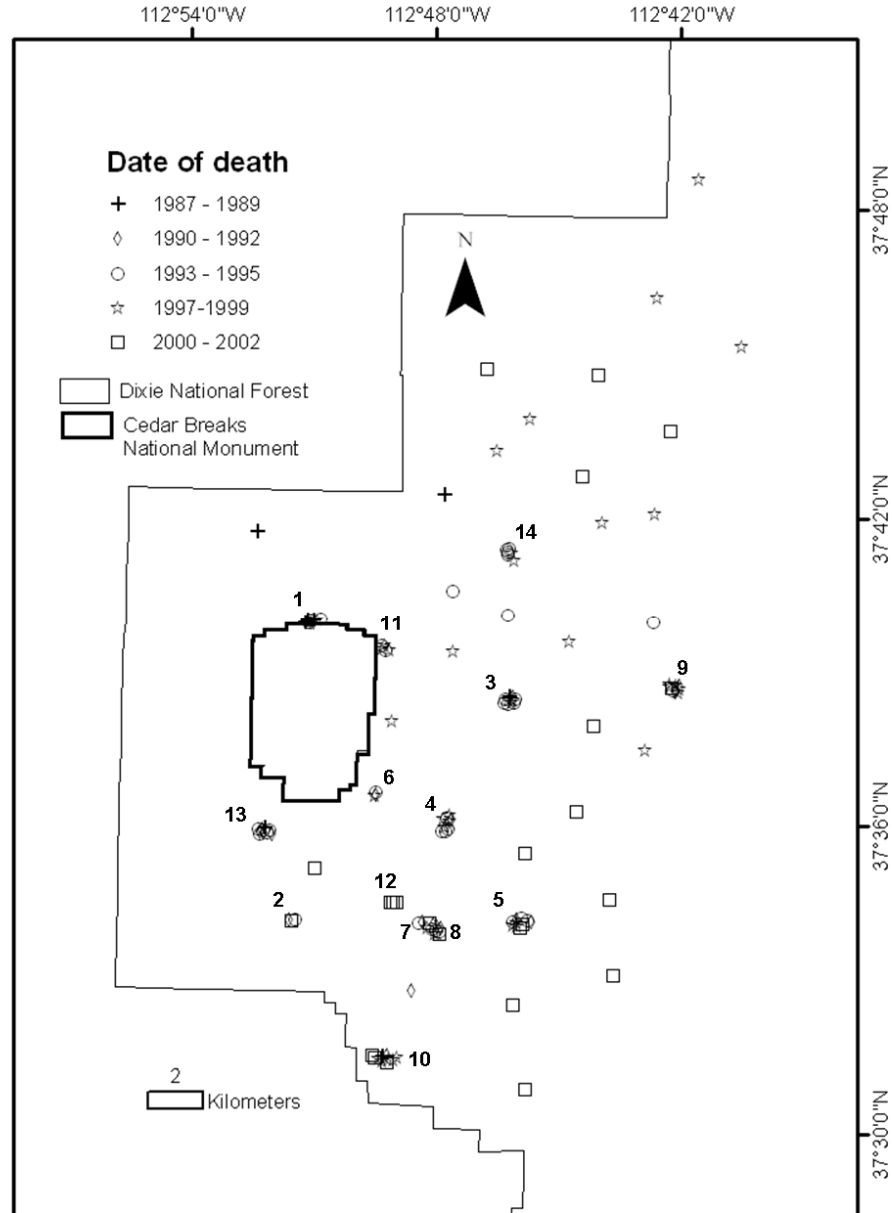


Figure 3.1. Spatiotemporal pattern of spruce beetle-killed Engelmann spruce plots ($n = 131$) on the Markagunt Plateau in southern Utah, USA. Symbols indicate first year a tree was killed by spruce beetle on that plot. Clumps of symbols labeled from 1 – 14 indicate intensively sampled study stands and individual symbols indicate extensively sampled plots (see Table 1 for stand names).

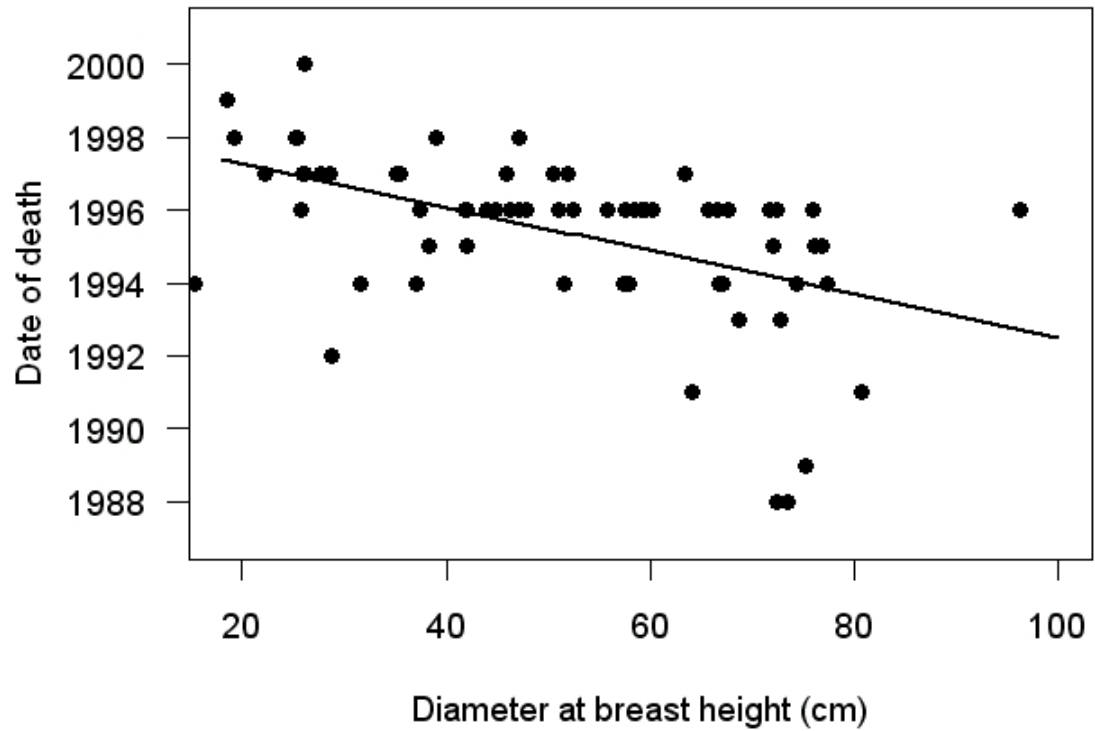


Figure 3.2. Relationship between timing of mortality and tree size ($r^2 = -0.49$, $P < 0.0001$) for the Ashdown stand.

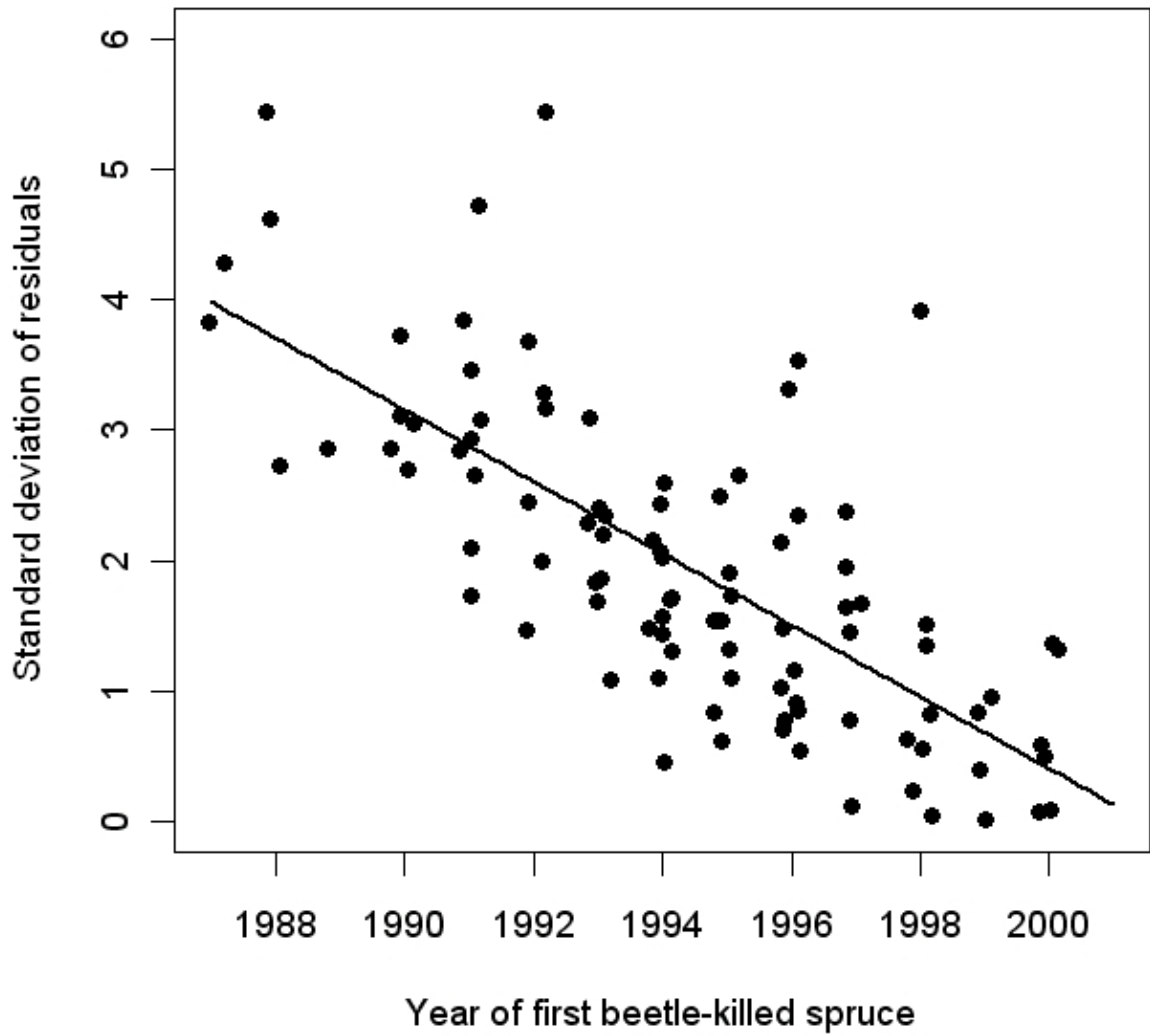


Figure 3.3. Standard deviation of residuals from the stand analysis as a function of the first year of spruce beetle attack by plot (Pearson $r^2 = -0.73$, $P < 0.0001$). Jitter was applied to Year of first beetle-killed spruce so overlapping observations were more visible.

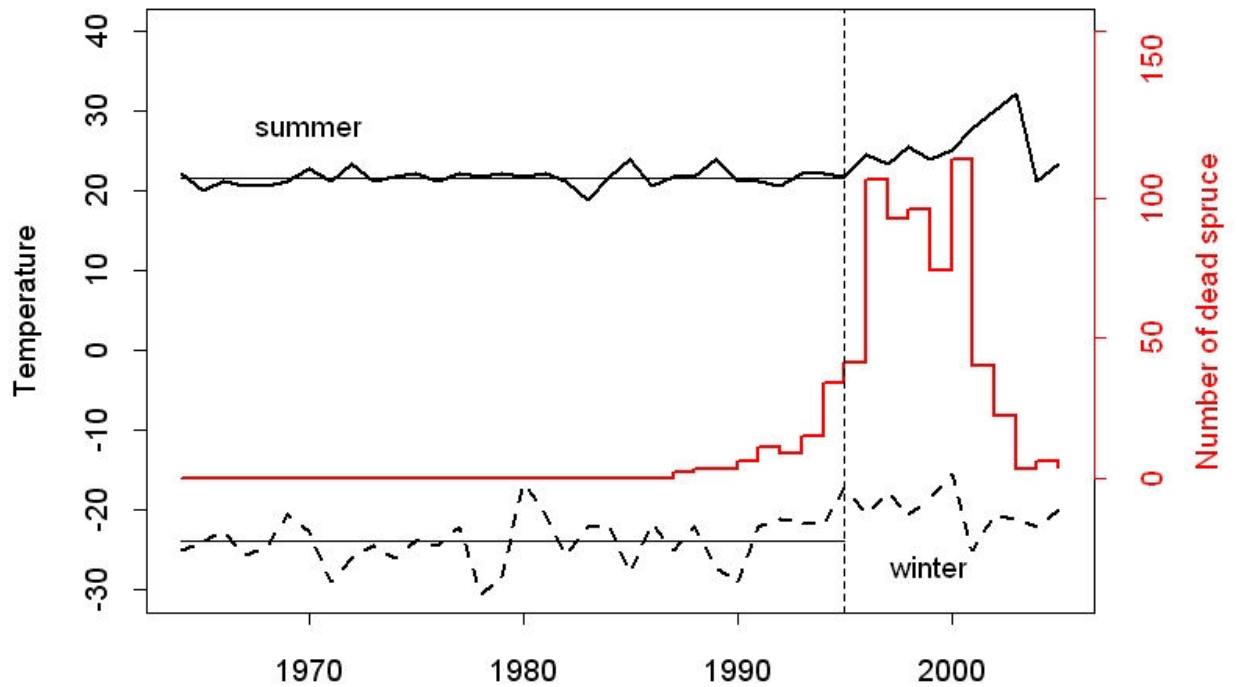


Figure 3.4. Summer (JAS) maximum and winter (JFM) minimum temperatures and their means (1964 – 1995) for the period 1964 -2005 showing deviation from long-term mean in ~ 1995 juxtaposed over frequency distribution of the number of spruce beetle-killed Engelmann spruce by year across the Markagunt Plateau. Dashed line indicates the boundary for calculation of long-term means (1964 – 1995).

CHAPTER 4

WILDFIRE AND SPRUCE BEETLE OUTBREAK: SIMULATION OF
INTERACTING DISTURBANCES IN THE CENTRAL ROCKY MOUNTAINS ^{5,6}*Abstract*

Infrequent, large-scale, natural disturbance regimes are an integral component of Engelmann spruce (*Picea engelmannii*) forests of the central Rocky Mountains. Wildfires, bark beetle outbreaks, winds, and avalanches cause relatively drastic changes in community structure, composition, and function. These disturbances may occur independently, or interact where the incidence of one may change the potential for another. We assessed potential wildfire behavior change in the wake of a catastrophic, landscape-wide, spruce beetle (*Dendroctonus rufipennis*) outbreak in southern Utah, USA. Using data collected in spruce forests affected by the outbreak, the Forest Vegetation Simulator and Fire and Fuels Extension were used to simulate long-term (100 y) stand dynamics and potential fire behavior under three reconstructed scenarios: no spruce beetle outbreak (low-severity), 50% spruce beetle-caused mortality (mid-severity), and 95% spruce beetle-caused mortality (high-severity). Simulations suggested a likely reduction in probability of active crown fire for one or two decades on near-pure Engelmann spruce sites after high-severity mortality. This counterintuitive result suggested extreme fire behavior is not an inevitable consequence of spruce beetle outbreaks. No change in potential fire behavior was predicted in stands with the least

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⁶ Coauthored by R. Justin DeRose and James N. Long.

reduction in spruce basal area (low- or mid-severity). In one stand with a history of surface fire, stand structure and potential fire behavior from low- and high-severity simulations were influenced by surface fire ~ 100 y ago. These results are indicative of complex disturbance interactions which were influenced by the host-specific spruce beetle, resultant stand structures and fuels profiles, and in one case antecedent disturbance.

Introduction

Large-scale disturbances are major ecosystem processes shaping community patterns in forested subalpine systems. Stand-replacing fire has received the most attention and is typically implicated as the primary disturbance factor for subalpine forests of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) (Peet, 2000). Recently however, the spruce beetle (*Dendroctonus rufipennis* Kirby) has been effecting large areas of Engelmann spruce forests across the western U.S. and Alaska (Veblen *et al.*, 1991; Berg *et al.*, 2006; DeRose & Long, 2007). Epidemic populations of the spruce beetle dramatically affect community composition and structure which, in turn, may influence community response to future disturbance (Baker & Veblen, 1990; DeRose & Long, 2007). Increasingly, disturbance interactions have become a focus of interest in disturbance ecology (Veblen *et al.*, 1994; Schoennagel, Veblen & Romme, 2004; Kulakowski & Veblen, 2007). In particular, the change in fire behavior in post-beetle outbreak forests is a topic of considerable interest (Romme *et al.*, unpublished report; Crawley, unpublished report).

Multiple hypotheses of disturbance interactions for Engelmann spruce forests exist. However, there is little consensus concerning connections between extreme wildfires and spruce beetle outbreaks. For example, Bigler, Kulakowski, and Veblen (2005) provided evidence that in a severe 2002 fire in a subalpine forest in western Colorado, probability of severe fire was only slightly increased in areas affected by the 1940s spruce beetle outbreak; instead, in areas burned in the late 1800s which resulted in stand structures and cover types less susceptible to burning, the extent of severe fire was strongly reduced. Also in western Colorado, both watershed-scale (Veblen *et al.*, 1994; Kulakowski, Veblen & Bebi, 2003) and regional-scale (Bebi, Kulakowski & Veblen, 2003) analyses did not support the general expectation of increased fire occurrence following the 1940s spruce beetle outbreak that killed most mature Engelmann spruce in the White River National Forest (Schmid & Frye, 1977). Similarly, analysis of the extent and severity of 2002 fires in western Colorado in areas affected by the late 1990s spruce beetle outbreak (i.e. during the red-needle and grey-needle phases) did not show an increase in either fire extent or severity in beetle-killed forests (Kulakowski & Veblen, 2007). Again, among variables related to stand conditions, stand origin following late 19th century fires was the strongest predictor of (reduced) fire extent. Although low-severity surface fires are not believed to be widespread in spruce-fir forests in Colorado, Kulakowski, Veblen and Bebi (2003) found that the 1940s spruce beetle outbreak reduced stand susceptibility to low-severity fire, perhaps due to increased moisture in the forest floor. A more general pattern of severe fires creating young post-fire spruce-fir stands that mitigate against spruce beetle attack for at least 70 y has been widely documented in western Colorado (Veblen *et al.*, 1994; Kulakowski, Veblen & Bebi, 2003; Kulakowski & Veblen, 2006). It

is apparent that potential interactions between wildfires and spruce beetle outbreaks in Engelmann spruce forests are both complex and not completely understood (Jenkins *et al.*, 2008).

Forest composition and structure prior to a spruce beetle outbreak in combination with host-specific mortality influences the short- mid- and long-term changes in fuels profiles. A rapid decrease in foliar moisture content occurs in the short-term (2-3 y). More profound changes to canopy fuels occur in the mid-term (one to many decades) due to the reduction in live spruce density which shifts the distribution of canopy foliage to subcanopy, non-host species (*e.g.* aspen (*Populus tremuloides*) and subalpine fir. As a result both canopy base height (CBH) and canopy bulk density (CBD) are reduced. Longer-term (many decades to centuries) influences include the addition of beetle-killed trees to the surface fuel load and changes in CBH and CBD associated with the density, composition, and growth of the understory trees.

These changes in the fuels profile affect potential fire behavior (Table 4.1). Potential surface fire intensity and flame length will increase through time as dead trees enter the surface fuel pool. Passive crown fire behavior where individual trees may “torch”(Scott & Reinhardt, 2001), is influenced by flame lengths and post-outbreak reductions in CBH. Torching is necessary to initiate active crown fire, which can be maintained if CBD is sufficient (Agee & Skinner, 2005). Alternatively, conditional fire behavior occurs when CBD is sufficient for active crown fire but flame lengths are too low, or CBH is too high for initiation of passive crown fire (Scott & Reinhardt, 2001). Potential fire behavior associated with post-beetle outbreak changes in the fuels profile can be evaluated under extreme fire weather using three criteria (Reinhardt, Crookston & Rebain, 2003): 1)

flame length indicates the intensity of surface fire and, in combination with CBH, whether passive crown fire behavior is likely, 2) Torching index (TI, $\text{km}\cdot\text{h}^{-1}$) is indicative of passive fire potential, 3) Crowning index (CI, $\text{km}\cdot\text{h}^{-1}$) is indicative of active crown fire potential.

We examined potential interactions between two extremely important types of disturbance in Engelmann spruce forests. Fire behavior predictions incorporate forecasts of stand dynamics to characterize the effects of changes in canopy and stand structure as a result of the spruce beetle outbreak. Three scenarios, representing different levels of spruce beetle impact, were developed to simulate potential fire behavior across a range of Engelmann spruce stand structure, composition, and fuel loading. The first scenario simulated potential fire behavior for mature, Engelmann spruce forest structure with little to no spruce beetle-caused mortality (low-severity). A second scenario simulated the effect of changed canopy fuels as a result of a spruce beetle outbreak (high-severity, >95% spruce mortality) on potential fire behavior. The third scenario examined the effect of canopy fuels changes associated with intermediate levels of spruce beetle-caused mortality (mid-severity, ~50% spruce mortality). To explore interactions between disturbances we posed the question is a high-severity spruce beetle outbreak likely to increase or decrease subsequent potential fire behavior? Disturbance interactions were indicated by changes in potential fire behavior as a result of the various levels of spruce beetle mortality and were based on modeled predictions of crowning and torching indices (Table 4.1).

Methods

STUDY AREA

This study was conducted in high-elevation Engelmann spruce forests on the Dixie National Forest on the Markagunt Plateau (DeRose & Long, 2007). It is one of several southern Utah plateaus dissected by rivers draining the western edge of the greater Colorado Plateau. The Markagunt Plateau is ~20 km east of Cedar City, Utah and the Engelmann spruce forests range from 2700 - 3300 m asl. In the early 1990s endemic populations of spruce beetle built to incipient levels and within a few years a full blown outbreak was underway that eventually moved across the entire plateau. Engelmann spruce mortality was severe and shifted forest dominance to subalpine fir and aspen (DeRose & Long, 2007).

Winter snowfall from the west and summer monsoons from the southeast (Mock, 1996) bring bimodal annual precipitation to the Markagunt and other southwestern Utah plateaus (Aquarius, Paunsaugunt, Sevier). This distribution of annual precipitation has likely had a large influence on historical fire occurrence (Figure 4.1).

Five study sites that were dominated by Engelmann spruce prior to the outbreak were studied (Table 4.2). Ashdown is located just to the north of Cedar Breaks National Monument and Snotel, just south, both had an understory of gooseberry (*Ribes montigenum*) and aspen bluebells (*Mertensia arizonica*). Bristlecone Pine Trail, Midway, and Navajo Lake, located southeast of Cedar Breaks, had minimal herbaceous vegetation. These sites represent a range of pre-outbreak Engelmann spruce composition, structure, and fuel loading (Tables 4.2 and 4.3).

FIRE WEATHER AND FUEL MOISTURE

Wind speed, temperature, and fuel moisture associated with extreme fire weather were reconstructed using the local Remote Automated Weather Station (RAWS) historical weather data from Aqua Canyon for years 1990 – 2006 (archived data at www.fs.fed.us/land/sfas.html) (Table 4.4). Fire Family Plus (<http://www.fire.org/>) was used to calculate wind speed, temperature, and fuel moisture content associated with historical extreme weather (97th percentile). One-min wind speed gusts were estimated from RAWS 10 min sustained wind speed measurements using NOAA tables (<http://www.seawfo.noaa.gov/fire/olm/fire/10togust.htm>).

CANOPY, UNDERSTORY, AND SURFACE FUEL MEASUREMENTS

Between four and 10 prism plots (basal area factor = $3.0 - 8.0 \text{ m}^2$, held constant for each site (Bell & Dilworth, 2002)) were measured on a grid pattern established with a randomly located starting point and at least 100 m apart. On each plot every tree was recorded for species, status (alive, dead, and cause of mortality), diameter at breast height (DBH, 1.3 m), height (HT), and height to the base of the live crown (CBH). For the spruce beetle-killed Engelmann spruce trees, CBH was estimated based on the height at which fine branches were retained. Special care was taken to differentiate whether an Engelmann spruce had been killed by the recent spruce beetle outbreak, past spruce beetle mortality or another agent. Recent mortality was noted by the presence of beetle galleries and sloughing bark whereas past beetle mortality was indicated by beetle galleries on grey boles and the general absence of bark. Other agents were identified by the absence of spruce beetle galleries. Increment cores taken to the pith at 5 - 30 cm

above ground level were returned to the lab and processed using standard core preparation techniques (Stokes & Smiley, 1968). Conservative estimates of age and 10 y diameter increment were determined by counting rings. Slope, aspect, and elevation were recorded for each plot.

At the center of each prism plot a 2 m radius fixed-area subplot was delineated and every tree less than 5 cm DBH was identified by species and measured for HT and diameter at the root collar. These understory trees were sectioned at ground level, taken to the lab, and processed using standard preparation techniques (Stokes & Smiley, 1968). Conservative estimates of age were determined by counting rings.

Surface fuel loading included all dead woody debris and was tallied by diameter classes at each plot (see below) using the planar transect method (Brown, Oberheu & Johnston, 1982) (Table 4.3). One h and 10 h fuels were measured along a 2 m transect, and 100 h on a 4 m transect. All debris > 7.63 cm (1000+ h moisture time-lag, coarse woody debris (CWD)) was measured along a 30 m transect. Species and condition (sound or rotten) were noted when discernable. Fuel bed depth, height of the tallest surface fuel up to 2 m, was measured at three points along each transect. Duff depth and litter depth were measured every 3 m along each transect (10 times). Five digital photographs per plot were taken to complement the fuels transects when identifying fuel models. Fuels Management AnalystTM (Carlton, 2006) was used to reduce surface fuel data to appropriate classes for model input (Table 4.3).

DATA ANALYSIS

We explored possible interactions between spruce beetle outbreaks and subsequent fire using field-collected data to parameterize models of forest stand dynamics and fire and fuel behavior. The Forest Vegetation Simulator (FVS) and its Fire and Fuels Extension (FFE), allow multi-year predictions of stand and fuel dynamics, and potential fire behavior. All data were imported into FVS for analysis and modeling. FVS is a deterministic, distance independent, individual tree, growth and yield model developed from region- and species-specific allometric equations (Crookston & Dixon, 2005). In FVS density related tree mortality is predicted using relative stand density index whereas density-independent mortality must be invoked by the user, e.g. with FFE. FVS is able to calibrate HT and large tree diameter growth with measurements of HT, crown ratio ((HT – CBH)/HT), site index, and 10 y diameter increment (Dixon, 2002). Site index (an integrative measure of site quality based on height and age of dominant trees) was calculated from six dominate Engelmann spruce from each site (Alexander, 1967). Regeneration does not occur automatically in FVS, rather it relies on user supplied data input at appropriate time-steps. Understory stocking and age data were used to estimate past natural regeneration by species and 10 y age classes; these estimates were used by FVS to simulate future regeneration for each site. Site-level analyses were performed using data averaged across plots.

FFE is an integrative fire behavior model incorporating surface fire models (Rothermel, 1982), crown fire initiation models (Van Wagner, 1977), and representative fuel models (Albini, 1976; Anderson, 1982; Scott & Burgan, 2005) to simulate natural and prescribed fire behavior. FFE combines stand growth simulation data from FVS with

fuel data to make predictions of potential fire behavior (Reinhardt, Crookston & Rebain, 2003) (Table 4.1). After every cycle of growth in FVS, stand level data are handed-off to FFE, which updates fuels profiles (Johnson, Peterson & Raymond, 2007). For example, if tree mortality occurs during a simulation this will be reflected in calculations of CBD and CBH by FFE. However, FFE does not take into consideration the red-needle stage of beetle outbreaks where dry needles remain on the tree. Likewise, variations in wind speed associated with stand density are not explicitly considered by FFE. Similarly, canopy foliar moisture is not directly considered instead CBD is used. The model can be enhanced with user defined variables for fuel loading, fire weather, and rate of snag fall. Measurements of surface fuel are not used directly for fire behavior predictions rather they are used to define one of the fuel models (see below, Scott & Burgan, 2005); users can specify a combination of fuel models. Neither FVS nor FFE take explicit consideration of herbaceous and grass growth and associated fuel loading; instead, fire behavior predictions are driven by overstory and understory trees and fuel models.

Stand dynamics and potential fire behavior were evaluated for three scenarios of spruce mortality severity: 1) a low-severity scenario was reconstructed from field data and represented forest conditions immediately prior to the 1990s spruce beetle outbreak, including trees killed prior to the recent outbreak; 2) a high-severity scenario characterized forest conditions 6-10 y following the spruce beetle outbreak and; 3) an alternative reconstructed spruce beetle outbreak scenario with ~ 50% mortality (mid-severity). Forest structure for the low-severity scenario was recreated by changing the status of all Engelmann spruce killed by the recent spruce beetle outbreak to live. Field data were used to simulate the high-severity scenario (~95% spruce mortality) (DeRose

& Long, 2007). The mid-severity scenario was created by modifying the reconstructed low-severity data to reflect 50% mortality of large diameter Engelmann spruce, consistent with the spruce beetle literature (Schmid & Frye, 1977; Holsten *et al.*, 1999). Since the outbreak was recent (Table 4.2) small changes in fire behavior as a result of changes in diameter increment of live trees post-outbreak are inconsequential. Increased fuel bed depth as a result of the spruce mortality is likely for 2-3 y post-outbreak; however, very little needle litter was observed on fuel transects which suggested rapid needle decomposition. Virtually all the Engelmann spruce killed in the outbreak were still standing.

FUEL MODELS

Fuel models integrate surface fuel load, bulk density and moisture of extinction in a mathematical representation for fire behavior predictions, *e.g.*, FFE (Scott & Burgan, 2005). These simplified fuel models allow the use of Rothermel's (1982) fire spread equations. As a result, fire behavior models are highly influenced by fine fuels, whereas the amount of CWD makes little difference on initial fire spread: grass, shrubs, or herbaceous plants will affect fire spread more than CWD. Originally, Rothermel (1982) identified 11 fuel models which were subsequently improved by Albini (1976) and most recently enhanced by Scott and Burgan (2005). These fuel models describe fuel characteristics during the most extreme periods of the fire season (Anderson, 1982). We used the newly developed fuel models of Scott and Burgan (2005) and one of the original models from Anderson (1982) in this study since these, used in combination, are most likely to accurately predict surface fire characteristics. We used plot photos and surface

fuel loading estimates (Table 4.3) to determine the major carrier of fire *e.g.*, herbaceous, shrub, conifer litter, etc. and defined site-specific fuel models (Scott & Burgan, 2005).

FIRE MODELING

All fire simulations were run with FVS/FFE for 100 y. For each scenario, we evaluated the predicted fire behavior under extreme fire weather conditions (*i.e.*, wind speed, fuel moistures, air temperature and humidity at the 97th percentile). The primary difference between the scenarios was the number of dead Engelmann spruce modeled as live. We only reconstructed Engelmann spruce trees determined to have been killed by the spruce beetle during the recent outbreak. Therefore stands in the low-severity scenario included a small percentage of standing dead spruce previously killed by spruce beetle or another agent (Table 4.2). Slopes of fuels transects were averaged over all plots for FFE input. The SnagFall keyword was used to simulate the rate of snag fall based on observations in southern Utah, *i.e.*, ~ 0.06% per y (Mielke, 1950). FFE default values of shrub and herbaceous fuel loading were used. The temperature, wind speed, and fuel moistures associated with extreme fire weather (Table 4.4) were entered into FFE.

Results

LOW-SEVERITY SCENARIO

Results from the low-severity scenario indicated torching and crowning were possible throughout the 100 y simulation in all stands but one (Bristlecone Pine Trail, see below) (Figure 4.2a) and with the exception of one decade (2026) in which conditional fire behavior was predicted for another stand (Snotel). Torching and crowning are likely when TI and CI are predicted to be below the critical wind speed threshold (Table 4.1).

Predicted torching and crowning were promoted by the high CBD associated with live canopy foliage (Figure 4.3a), coupled with low CBH characteristic of substantial ladder fuels (Figure 4.3b), and sufficiently long FL (Figure 4.3c) for surface fire to enter the canopy. Thus, with the exception of the Bristlecone Pine Trail stand (see second-order disturbance interaction below), spruce stand structures in the low-severity scenario were associated with the potential for crown fire on all sites throughout the simulations (Figure 4.2a).

MID-SEVERITY SCENARIO

Similarities in CBD, CBH, and FL between the low- and mid-severity scenarios (Figure 4.3) suggested little difference in predicted fire behavior (Figure 4.2a-b). Like the low-severity scenario, the mid-severity scenario showed the potential for torching and crowning throughout the simulation on all sites, except Bristlecone Pine Trail (Figure 4.2b), with the exception of two decades (2086 and 2096) in which conditional fire behavior was predicted for Snotel. Conditional fire behavior occurs when crowning is likely, but torching is not (Table 4.1).

HIGH-SEVERITY SCENARIO

For the high-severity scenario only sites with relatively pure Engelmann spruce composition resulted in reduced TI and CI for a couple of decades (Ashdown and Snotel, Figure 4.2c, Table 4.2). Therefore, a threshold in spruce composition exists beyond which a high-severity beetle outbreak may actually result in reduced crown fire behavior. Below this threshold low- to mid- to high-severity comparisons of CBD, CBH, and FL (Figure 4.3) revealed little difference between scenarios for Midway and Navajo Lake.

Both sites exhibited crowning and torching fire behavior regardless of the spruce mortality scenario. Therefore a lower percentage of spruce composition prior to an outbreak resulted in little change in potential fire behavior between low- and high-severity spruce beetle mortality.

SECOND-ORDER DISTURBANCE INTERACTION

In an unusual case, forest structure at Bristlecone Pine Trail influenced the 1990s beetle outbreak, but not scenarios of low- or high-severity fire behavior. Conditional fire behavior was predicted for both the low- and mid-severity scenarios, except for the three final decades (2076-2096) in the mid-severity scenario where torching was possible. Low TI values (Figure 4.2) were likely due to regenerating trees and associated fuel loading which resulted in a gradual reduction of CBH. Crowning is unlikely in the high-severity scenario but for 2026-2046 torching is possible, probably associated with reduced CBH in 2026 (Figure 4.3b). Even under extreme weather it is likely only a surface fire would occur on Bristlecone Pine Trail due to the combination of high CBH and low FL (Figures 4.3b-c). Bristlecone Pine Trail had sufficient CBD to maintain a crown fire for the low- and mid-severity scenarios (Figure 4.3); however, extremely high CBH (Figure 4.3b) suggested crowning is unlikely. In the high-severity scenario a combination of relatively low CBH and relatively long FL would indicate the possibility for crown fire; however, drastic reduction in CBD due to the severe spruce mortality associated with this scenario suggests only surface fire is likely.

Discussion

LOW-SEVERITY SCENARIO

Pre-outbreak (low-severity scenario) Engelmann spruce forest structure and species composition influenced predictions of fire behavior. Bigler, Kulakowski, and Veblen (2005) found the probability of high severity fires after spruce beetle outbreaks was highly influenced by stand structure (young versus old) which is not inconsistent with our results. In general, pre-outbreak (low-severity) mature, Engelmann spruce forests are much more likely to exhibit torching and crowing, under extreme fire weather conditions, as a result of their relatively continuous horizontal and vertical fuel distribution (except Bristlecone Pine Trail).

MID-SEVERITY SCENARIO

Predictions of fire behavior under the mid-severity scenario were not intermediate to low- and high-severity scenarios but rather deviated only slightly from the low-severity scenario (Figure 4.2). The relatively diverse composition in Midway and Navajo Lake resulted in smaller differences in CBD such that crowning and torching fire behavior were likely regardless of spruce mortality (low-, mid-, or high-severity). Furthermore, a dense understory of aspen and subalpine fir ensured CI and TI stayed below the critical wind speed threshold throughout the simulations (Figure 4.2). Similarly, the modeled understory regeneration accentuated the vertical canopy structure and ensured consistently high CBD and low CBH (Figure 4.3a-b), both exacerbating torching and crowning.

HIGH-SEVERITY SCENARIO

Extreme fire behavior is not an inevitable consequence of spruce beetle epidemics. Under the high-severity scenario, our simulations predicted reduced crown fire behavior (high CI and TI) for stands that had relatively pure spruce composition prior to the outbreak (Ashdown and Snotel, Table 4.2). This counterintuitive result was likely driven by substantial reductions in CBD (Figure 4.3a) associated with the host-specific spruce beetle outbreak. Even though severe spruce mortality in relatively pure stands ‘looks’ more flammable, stands Ashdown and Snotel under the high-severity scenario had few residual live trees, a reduction in horizontal crown continuity, and an understory of primarily herbaceous plants which resulted in many decades of reduced crown fire behavior. Under these conditions surface fire is possible, but crown fire is unlikely, even under extreme weather conditions, until substantial regeneration develops. Consistent with our results, Bebi, Kulakowski, and Veblen (2003) found low elevation subalpine forests were not more susceptible to subsequent fire than areas without a history of spruce beetle outbreak. Similarly, Kulakowski, Veblen, and Bebi (2003) found that low-severity fires post-beetle outbreak were much more common in stands with <19% beetle mortality, whereas stands with >60% mortality had fewer fires than expected. This is similar to the results from our high-severity scenario for Ashdown and Snotel which had >95% spruce mortality and reduced crown fire behavior. High-severity simulations showed mid-term (2-3 decades) crowning is unlikely in Ashdown (2006) and Snotel (2006-2016). However, after 4-5 decades, development of a regenerating understory (increasing CBD, Figure 4.3a) resulted in a decrease in both TI and CI and increased the likelihood of active crown fire. Furthermore, long FL for both sites, a result of the

increased herbaceous fuel loading, resulted in the possibility of torching for the first 6 or 7 decades of the simulation (Figure 4.3).

SECOND-ORDER DISTURBANCE INTERACTION

Bristlecone Pine Trail was an unusual example of a fire by spruce beetle by potential fire disturbance interaction. A human-ignited surface fire occurred on this site in *ca* 1906 (James Bowns, personal communication). Increment cores extracted from recently killed Engelmann spruce at Bristlecone Pine Trail corroborated that spruce regeneration followed the 1906 surface fire. Veblen *et al.* (1994), Bebi, Kulakowski, and Veblen (2003), and Kulakowski and Veblen (2006) documented a reduction in susceptibility to spruce beetle outbreak as a result of antecedent stand-replacing fires, where the youngest stands (~ 50 y) were the least susceptible. Although Bristlecone Pine Trail burned in 1906, the fire was not stand-replacing and likely acted only to reduce surface fuels and kill smaller trees while leaving many larger Douglas-fir and limber pine. Unfortunately, even the relatively young (~ 100 y old) spruce were entirely killed in the recent outbreak; the *ca* 70 y threshold before spruce are susceptible to the spruce beetle suggested by Veblen *et al.* (1994) for Colorado Engelmann spruce forests may also apply to southern Utah forests. The primary difference between Bristlecone Pine Trail and the others sites appears to be the dearth of understory trees and herbaceous species. The loss of understory trees to fire in 1906 resulted in a much higher CBH (Figure 4.3) even after 100 y, which undoubtedly contributes to the unlikelihood of torching at Bristlecone Pine Trail. Therefore, the 1906 surface fire reduced understory stocking and ladder fuels which resulted in spruce regeneration that, after ~ 100 y, was susceptible to the beetle

outbreak; however, it was the initial reduction in understory stocking and ladder fuels, not the outbreak per se, which influenced fire behavior predictions. This provides evidence for a second-order disturbance interaction.

FVS / FFE MODELING CHALLENGES

The increase in herbaceous fuel loading following bark beetle outbreaks found in many forest types (McCambridge *et al.*, 1982; Holsten *et al.*, 1995; Stone & Wolfe, 1996; McMillin & Allen, 2003) was also evident in Ashdown and Snotel. To account for the higher FL associated with increase in herbaceous species during modeling, a combination of fuel models was used (Table 4.3). We simulated each stand with a 30% contribution from fuel model 2, which has relatively longer flame lengths than fuel model SB1. This resulted in longer FL early in the simulations (Figure 4.3c). Failure to take into account the increased herbaceous loading during simulations would have result in increased CI and TI for many more decades. Similarly, recent work in lodgepole pine stands suggested fine fuel loading <5 y after mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks increased significantly, purportedly due to needle and twig drop, and this increase could lead to increased rates of spread and surface fire intensity (Page & Jenkins, 2007a,b). While it is possible our estimates of fine fuel were influenced by the recent needle drop associated with the outbreak (i.e. 6-10 y prior), needles were not readily apparent on fuel transects. Furthermore, fuels transect data are not used directly for fire modeling (see Data analysis above), but rather their distribution across diameter classes is used, in part, to identify appropriate fuel models. Based on our surface fuel

loading (Table 4.3) it is unlikely an increase in fine fuels would lead to the assignment of different fuel models.

Another modeling challenge associated with FFE is that it does not take into account the relatively short-duration retention of foliage post-outbreak (*e.g.*, 2-3 y for Engelmann spruce (Holsten *et al.*, 1999)). Potential fire behavior might spike during this short window, mostly due to decreased moisture in the crown. On the Markagunt Plateau, during the short time between the spruce beetle attack and the complete loss of needles and fine branches, there were no severe fires (Fire occurrence data, <http://famweb.nwcg.gov/weatherfirecd/utah.htm>). Similarly, Kulakowski and Veblen (2007) did not find support for greater fire severity 2-3 y after spruce beetle attacks. This short window likely represents the only time when crown fire might be more likely, given extreme fire weather, in pure Engelmann spruce sites affected by a high-severity beetle outbreak (*e.g.*, Ashdown or Snotel).

POTENTIAL FIRE, FUELS, AND WEATHER

Given enough time it is possible for extreme fire weather, ignition, and sufficient fuels to occur simultaneously resulting in extreme fire behavior in these Engelmann spruce forests. Past occurrence of small, natural and human caused fires on the Markagunt Plateau was primarily during the driest season, prior to summer monsoons (Figure 4.1). It is likely that this landscape has been without extreme, large-scale fire for many centuries (DeRose & Long, 2007). Although charcoal was ubiquitous on the plateau, the amount found varied by site (unpublished data), could be many 1000s of y old, and could be influenced by young lava flows (*ca* 1000-3000 y BP, Moore *et al.*,

2004). A study of bog sediments from lower elevation, mixed-conifer forests on the Markagunt Plateau suggested an average fire return interval of 330 – 410 y (Madsen *et al.*, 2002) but this localized analysis may not characterize higher elevation Engelmann spruce-dominated forests. It is clear fuel loading necessary for crown fire existed prior to the outbreak (low-severity scenario), and in some cases after the outbreak. Therefore, extreme fire weather and ignition must be limiting the occurrence of fire in this system. Bessie and Johnson (1995) found that both surface fire intensity and crown fire initiation were more strongly related to extreme fire weather than to fuel loading in subalpine forests and Sibold *et al.* (2006) and Schoennagel *et al.* (2007) found evidence for this in Colorado. We found extreme fire weather is necessary for burning on the Markagunt Plateau but critical thresholds for fuel loading and stand structure must also be met. It appears that, in general, the change in fuels profiles and species composition between pre-outbreak (low-severity) and post-outbreak (high-severity) forests on the Markagunt Plateau does not always result in increased potential fire behavior. Instead on some sites (*i.e.*, Ashdown and Snotel) a counterintuitive effect, reduced potential fire behavior, was the result.

Conclusions

Model simulations suggested pre-outbreak (low-severity) Engelmann spruce forest structure and composition influenced the spruce beetle outbreak, which subsequently affected predicted fire behavior on the Markagunt Plateau in southern Utah. Interactions between the outbreak and subsequent potential fire behavior were related to Engelmann spruce composition: 1) at sites with lower spruce composition (Midway and Navajo

Lake) the spruce beetle outbreak did not change canopy structure sufficiently to alter the potential for crown fire, 2) at sites with high spruce composition (Ashdown, and Snotel) the host-specific spruce beetle substantially reduced canopy fuel and therefore subsequent crowning potential for at least several decades, 3) in one site with a known surface fire history (Bristlecone Pine Trail), the influence of the beetle outbreak on canopy fuel load may have had little or no net effect on subsequent potential fire behavior indicating a second-order disturbance interaction. Our results are consistent with interactions of spruce beetle and subsequent fire behavior with the results heavily influenced by pre-outbreak Engelmann spruce composition. We conclude that extreme fire behavior is not an inevitable consequence of spruce beetle outbreaks.

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TABLE 4.1. Potential fire behavior types, rules for their occurrence, and evaluation criteria under extreme fire weather used in this study, from Reinhardt, Crookston and Rebain (2003).

Fire type	Description	Evaluation criteria
Surface	Flame length depends on fuel loading and fuel moisture content, spread influenced by slope and wind speed	Crowning index ^a and torching index ^b > critical wind speed ^c
Passive	‘Torching’ where individual trees or small groups of trees burn but solid flame is not maintained in the canopy, occurs when a critical wind speed is exceeded	Crowning index > critical wind speed and torching index < critical wind speed
Active	‘Crowning’ where both the surface and canopy burn, solid flame maintained from ground to canopy, occurs when a critical wind speed is exceeded	Crowning index and torching index < critical wind speed
Conditional	‘Crowning’ possible but limited by insufficient ladder fuels for surface fire to enter canopy	Crowning index < critical wind speed but torching index > critical wind speed

^aCrowning index is the wind speed necessary to maintain active crown fire.

^bTorching index is the wind speed necessary to ignite the canopy of individual-trees.

^cCritical wind speed is a threshold value, determined from extreme fire weather, which indicates whether fire can move from the surface to the canopy.

Table 4.2. Stand-level attributes of the five study sites.

Site	Latitude	Longitude	# plots	Approx. year of outbreak	Site Index ^b (m)	Average slope (percent)	Elevation (m asl)	Species composition ^a (percent basal area)						
								ES (PD)	ES (RD)	ES (L)	SF	AS	DF	LM
Ashdown	37°66'	112°84'	6	1996	13.4	2.5	3197	<1	78	8	14	-	-	-
Bristlecone Pine Trail	37°56'	112°85'	4	1999	15.2	28	3016	<1	65	3	8	-	22	2
Midway	37°56'	112°79'	10	1999	16.7	2	2977	<1	62	3	11	24	-	-
Navajo Lake	37°52'	112°81'	6	2000	17.6	21	2846	2	39	9	20	-	28	2
Snotel	37°59'	112°86'	5	1998	16.1	24	3229	3	86	3	8	-	-	-

^a Species composition at time of 2006 measurement including live (L), recently dead Engelmann spruce (RD), and pre-outbreak Engelmann spruce snags (PD), but not including standing dead of other species. ES – Engelmann spruce, SF – subalpine fir, AS – aspen, DF – Douglas-fir, LM – limber pine. ^b Site index base age 50 years.

TABLE 4.3. Surface fuel loading ($\text{Mg}\cdot\text{ha}^{-1}$), designated fuel model, and associated weights for each site on the Markagunt Plateau.

Site	0-0.64 (cm)	0.65- 2.54 (cm)	2.55- 7.62 (cm)	>7.63 (cm) sound	>7.63 (cm) rotten	Fuel bed depth (cm)	Fuel model ^a	Fuel model weight (percent)
Ashdown	0.76	4.53	10.9	3.6	35.1	17	2 / SB1	30 / 70
Bristlecone Pine Trail	2.13	6.43	8.3	23.6	20.5	6	SB1	100
Midway	1.57	6.41	8.1	20.8	23.9	10	TU5 / SB1	50 / 50
Navajo Lake	0.72	3.38	6.3	24.6	20.6	15	SB1	100
Snotel	0.38	5.89	3.2	2.8	48.2	7	2 / SB1	30 / 70

^a Fuel model definitions as defined by Albin (1976) and Scott & Burgan (2005).

TABLE 4.4. Fuel moisture content and fire weather data used for potential fire behavior modeling under extreme weather (97th percentile) in the Fire and Fuels Extension.

	97th percentile
1 h	1.9
10 h	2.1
100 h	3.2
1000 h	4.9
Live herbaceous	29.7
Live woody	60
Dry bulb temperature (C)	28
Maximum probable 1 m wind speed (km·h ⁻¹)	39

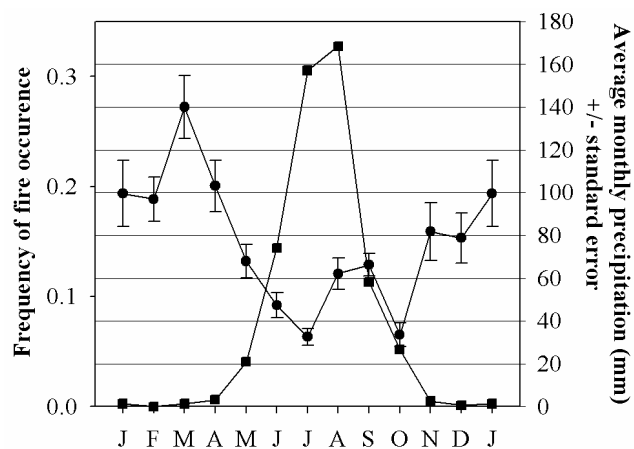


FIGURE 4.1. Average monthly precipitation (mm) +/- one standard error (●) for the Midway Valley Snowpack Telemetry (SNOTEL) site (37°56'N, -112°83'W, 2987 m elevation) from 1982 – 2005 and frequency of fires (■) on the Cedar City Ranger District from 1970 – 2006. Fire frequency data from fire occurrence files for the Dixie National Forest (<http://famweb.nwcg.gov/weatherfirecd/utah.htm>).

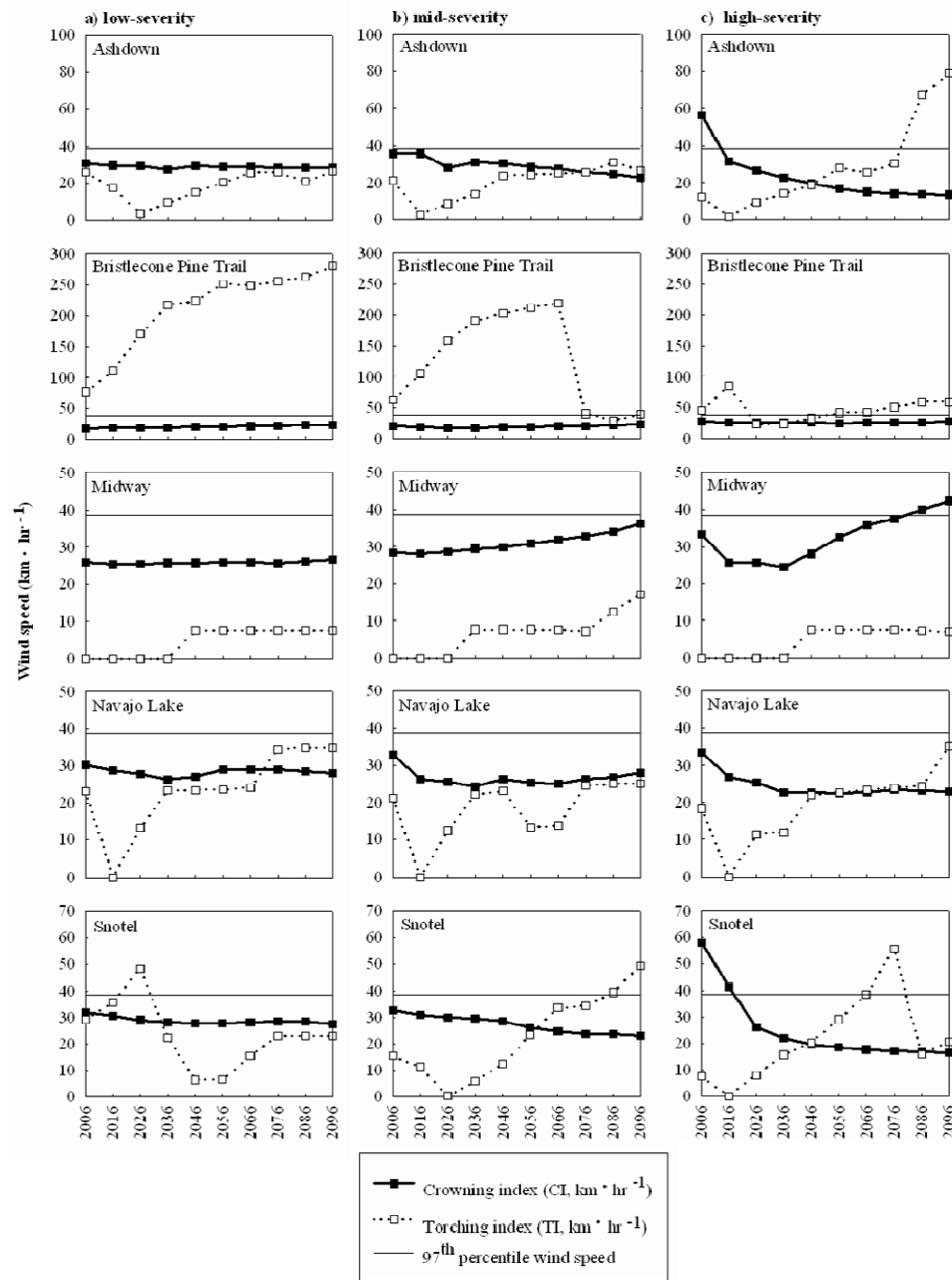


FIGURE 4.2. Crowning and torching indices ($\text{km} \cdot \text{h}^{-1}$) over the simulation period for the study sites under: a) endemic spruce beetle scenario, b) epidemic spruce beetle scenario, and c) post-epidemic spruce beetle scenario. Values above the 97th percentile wind speed (solid horizontal line) indicate unlikely torching or crowning. Values below indicate torching or crowning likely.

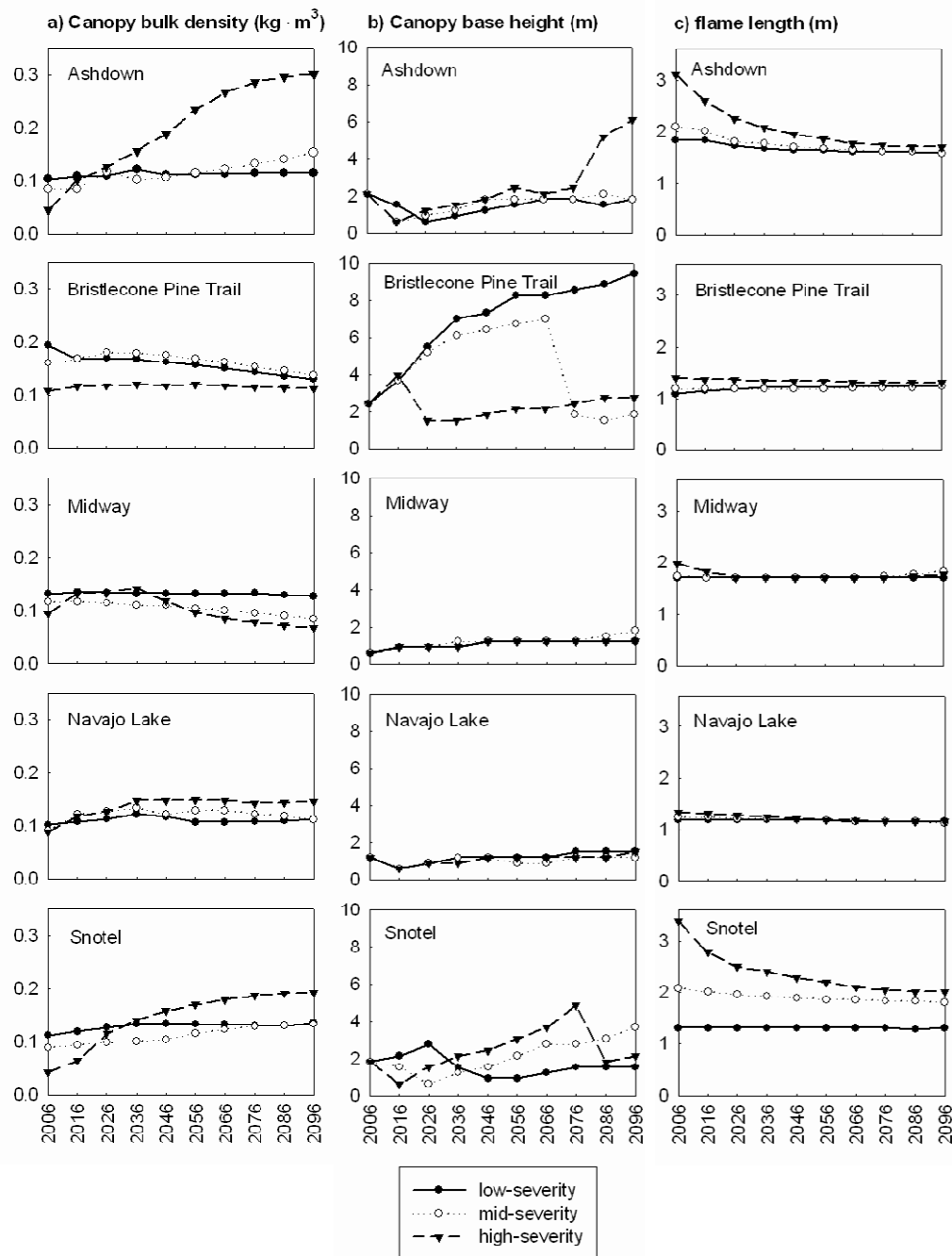


FIGURE 4.3. Canopy bulk density (kg·m⁻³) (a), canopy base height (dm) (b), and flame length (dm) (c) by site under each scenario (low-, mid-, and high-severity) for the simulation period (2006-2096).

CHAPTER 5

REGENERATION RESPONSE AND SEEDLING BANK DYNAMICS ON A
DENDROCTONUS RUFIPENNIS-KILLED *PICEA ENGELMANNII* LANDSCAPE ^{7,8}

Abstract

Question: How does regeneration response to a host-specific, high-severity, infrequent *Dendroctonus rufipennis* outbreak differ from our conceptualization of high-severity, infrequent / low-severity, frequent disturbance regimes in *Picea engelmannii* – *Abies lasiocarpa* communities?

Location: Southern Utah, USA.

Methods: 107 plots across a high-elevation *P. engelmannii* forest were sampled to reconstruct pre-outbreak overstory and seedling bank densities and calculate their associated metrics of diversity. Decade of establishment by seedling bank trees indicated ‘chronic’ and ‘pulse’ regenerators.

Results: The post-outbreak overstory and seedling bank were dominated by *A. lasiocarpa*. Although *Pinus flexilis*, *Pinus ponderosa*, *Picea pungens*, and *Psuedotsuga menziesii* were present in the overstory, they were virtually absent in the seedling bank. Seedling bank recruitment of *A. lasiocarpa* and *P. engelmannii* has been occurring chronically for at least the last ~ 205 yr and ~ 152 yr, respectively. A pulse response of seedling bank *Populus tremuloides* was apparent; however, results were complicated by intense ungulate browsing.

⁷ This chapter is in press in the Journal of Vegetation Science as: DeRose, R.J. and Long, J.N. Regeneration response and seedling bank dynamics on a *Dendroctonus rufipennis*-killed *Picea engelmannii* landscape.

⁸ Coauthored by R. Justin DeRose and James N. Long

Conclusions: Despite some similarities to the high-severity, infrequent / low-severity, frequent conceptualization of regeneration response to disturbance, the high-severity *D. rufipennis* outbreak is best described by explicitly considering host-specificity and severity. Although, the outbreak simultaneously promoted both a pulse of *P. tremuloides* and a release of chronically regenerated *A. lasiocarpa*, the *P. tremuloides* response was generally masked by ungulate browsing and regeneration response came overwhelmingly from the *A. lasiocarpa* seedling bank. In this landscape once dominated by *P. engelmannii* the chronically regenerating seedling bank, typically thought to take advantage of canopy gaps associated with low-severity disturbances, is poised to dominate forest reorganization in response to the host-specific outbreak.

Introduction

Regeneration response to disturbance is an integral part of forest stand dynamics and is commonly described as a function of the disturbance regime severity. Descriptors of disturbance magnitude such as severity (White & Pickett 1985) are inversely related to disturbance frequency (White & Jentsch 2001). Disturbance regimes are often characterized as high-severity and infrequent, low-severity and frequent, or mixed in severity and frequency (Turner et al. 2001). Characteristics of mixed-severity disturbances are intricately linked to gap size but are typically intermediate to high- and low-severity disturbances. Regeneration response to mixed-severity disturbance is extremely variable and is often called ‘gap phase’ (Veblen 1992). In this paper we explicitly focus on the comparison between regeneration response associated with high-severity and low-severity disturbances.

High-severity, infrequent disturbances typically create increased growing space, high light levels, expose mineral soil, and reduced competition (Oliver 1981). Early successional, shade-intolerant species respond to the rapid environmental change caused by the disturbance with a ‘pulse’ of regeneration. As a result, regeneration can be characterized as an event, with establishment occurring over a fairly short time period. In contrast, low-severity, frequent disturbances are commonly associated with limited growing space, low light levels, limited exposed mineral soil, and a high level of competition with existing vegetation (Veblen 1986). In response to low-severity disturbances, seedlings of late successional, shade-tolerant species, capable of existing in very low light conditions, gradually accumulate as advance regeneration beneath the overstory. This continuous, or ‘chronic’, establishment of regeneration can be characterized as a process whereby a seedling bank (i.e., trees < 5 cm diameter at breast height) gradually develops as advance regeneration in the absence of high-severity disturbance.

Disturbance regimes and their characteristic regeneration responses are typically associated with a particular forest type. For example, *Pinus contorta* var. *latifolia* forests are usually comprised of even-aged cohorts resulting from a high-severity, stand-replacing fire (Oliver 1981), whereas subalpine conifer forests in British Columbia are multi-aged as a result of frequent, low-severity mortality of canopy dominants (Lertzman & Krebs 1991).

Southern Rocky Mountain *Picea engelmannii* – *Abies lasiocarpa* communities are high elevation extensions of the boreal forest (Peet 2000) and are dominated by *P. engelmannii*, *A. lasiocarpa* and their common associates including: *Populus tremuloides*,

P. contorta, and less commonly *Pinus flexilis* and *Pseudotsuga menziesii* (Long 1994). These forests are typically many centuries old (Aplet et al. 1988); their origin usually attributed to high-severity, infrequent, stand-replacing fires that are indiscriminate with respect to species composition and result in large patches of mineral soil available for establishment (Bloomberg 1950). Shortly after a disturbance, early successional, shade-intolerant species such as *P. tremuloides* or *P. contorta*, which have biological legacies on-site (root stocks or canopy seed banks), are able to quickly establish the site. This establishment, representing a pulse of regeneration, results in domination by these species for 100 yr or more. In the long absence of another high-severity disturbance, a suite of disturbances such as root disease, bark beetles, and wind throw often act in combination to create small spatially separated gaps by causing species-specific mortality of individuals. The continuous creation of small patches favors chronic regeneration of shade-tolerant *P. engelmannii* and *A. lasiocarpa* in the seedling bank (Veblen 1986). Differences in gap creation can confer an advantage to one species or another e.g., exposed mineral soil associated with a tip-up mound will favor *P. engelmannii*. In contrast, *A. lasiocarpa* is more likely to establish without exposed mineral soil. The process of chronic regeneration will eventually result in a dense seedling bank.

Recently (1990s) a catastrophic (*sensu* Hardy 2005) *Dendroctonus rufipennis* outbreak occurred on the Markagunt Plateau in southern Utah. In this once *P. engelmannii*-dominated forest, the *D. rufipennis* outbreak resulted in nearly complete overstory mortality (DeRose & Long 2007). High-severity, *D. rufipennis* outbreaks (epidemics) selectively kill only overstory *P. engelmannii* leaving the non-host overstory and the seedling bank to respond. Regeneration response to *D. rufipennis* outbreaks and other

disturbances such as catastrophic wind are not adequately described by the conventional disturbance regime conceptualization, which does not take into account disturbance host-specificity.

In this study, we describe seedling bank dynamics and regeneration response in the wake of a host-specific, high-severity *D. rufipennis* outbreak. We analyzed species-specific age structures and growth dynamics of the seedling bank to ascertain whether the regeneration response to the outbreak was more characteristically a pulse (high-severity) or chronic (low-severity) disturbance. We also analyzed the influence of pre-outbreak, non-host overstory abundance and composition on the post-outbreak seedling bank to evaluate their roles in regeneration response.

Our objective is to characterize regeneration response to a *D. rufipennis* outbreak, determine how it may or may not differ from the high-severity, infrequent / low-severity, frequent conceptualization of disturbance regimes in *P. engelmannii* - *A. lasiocarpa* communities, and to determine how an extreme *D. rufipennis* outbreak may influence forest stand dynamics.

Methods

Study area

The study area is located in the subalpine *P. engelmannii* - *A. lasiocarpa* zone on the Dixie National Forest, Cedar City Ranger District, on the Markagunt Plateau in southwestern Utah (Fig. 5.1). Prior to the mid-1990s *D. rufipennis* outbreak, the forest was dominated by *P. engelmannii* (Fig. 5.2; DeRose & Long 2007). Minor components of the forest included *A. lasiocarpa* and *P. tremuloides* at higher elevations and *P. flexilis*,

P. menziesii, *P. pungens*, and *Pinus ponderosa* at lower elevations. Shrub species included *Ribes montigenum* and *Mertensia arizonica* with abundant *Artemisia* spp. in adjacent subalpine meadows. Elevation of the study sites ranged from 2600 – 3300 m asl (Table 5.1, Fig. 5.1). Tertiary deposits of the Claron Lake Formation are responsible for the reddish, silty soil over much of the western and northern parts of the plateau (Chronic 1990). Recent (1000-5000 yr BP) conspicuous basalt flows cover a large portion of the central part of the plateau and are underlain by Tertiary volcanic rock (Chronic 1990). Annual precipitation varied between 369 and 1709 mm over the period 1948-2005. Average annual temperature varied between -0.9 and 3.1 °C over the same period (<http://www.nrcs.usda.gov/>). A general description of regional climate for the plateau can be found in Chapter 4.

Field sampling

Study sites were carefully chosen where no evidence of past large-scale anthropogenic canopy disturbance was evident (i.e., logging). Each sampled stand appeared homogeneous in terms of overstory structure. Most stands were recently dominated by *P. engelmannii* with composition varying from ~50% to ~95% *P. engelmannii* basal area ($\text{m}^2 \text{ha}^{-1}$ at 1.3 m) prior to the outbreak (except for Rainbow Meadows and Sydney Valley, which were dominated by *A. lasiocarpa*). Past elevated beetle populations have been reported as early as 1937 (cited in Hebertson & Jenkins 2008), and a large-scale outbreak occurred during 1916-1918 ~ 120 km east-northeast of the study site on the Aquarius Plateau (Mielke 1950).

Depending on overall stand size, three to 10 plots were measured at each site during the summers of 2005, 2006, and 2007. A grid sampling network was established in each stand from a randomly located starting point and azimuth. Variable radius plot sampling was used to assess overstory trees (> 5 cm diameter at breast height (DBH)) (Bell & Dilworth 2002). DBH and height were measured for each overstory tree and species and status (live or dead) were noted. Since the outbreak was recent (1990s) nearly every beetle-killed tree was still standing ($\sim 99.2\%$); therefore, both live and dead standing trees were measured to indicate beetle-caused mortality (Veblen et al. 1991b). Rate-of-fall for beetle-killed *P. engelmannii* is thought to be site-specific (E.G. Hebertson, pers. comm., fall 2008, US Forest Service, Forest Health Protection Specialist) and the rate found on nearby Aquarius Plateau ($\sim 0.6\%$ per yr Mielke 1950) was consistent with our observations. *P. engelmannii* were examined to determine whether mortality was caused by the recent *D. rufipennis* outbreak, which would be indicated by the presence of beetle galleries on the surface of the bole and emergence holes in the bark. Although foresters often differentiate seedlings (< 2 m in height) from saplings (> 2 m in height but < 5 cm in DBH), for ease of interpretation in this study all trees > 5 cm in height and < 5 cm in DBH were referred to as the seedling bank. The seedling bank was measured on fixed-area subplots (1 m – 3 m radius based on site-specific seedling bank density) in the center of each overstory plot. Height and basal diameter were measured and species noted before cross-sections were removed at ground-level from every tree in the subplot, including root suckers of *P. tremuloides*. In the lab, cross-sections were sanded with progressively finer sandpaper before annual rings were counted under a microscope.

A total of 2093 seedling bank trees were measured in 107 plots on 14 sites across the plateau and used for abundance estimation and comparisons of the overstory composition to seedling bank composition (Table 5.1). Of these trees, 1850 were successfully aged. In order of abundance they were: *A. lasiocarpa*, 1535 (83%); *P. tremuloides* 249 (13%); *P. engelmannii*, 62 (4%); *P. pungens*, 3 (<0.01%); and *P. ponderosa*, 1 (<0.001%). Seedling bank age structure and height - age relationships were analyzed using 1846 of these trees (three *P. pungens* and one *P. ponderosa* were removed). Although found in the overstory, neither *P. menziesii* or *P. flexilis* were present in the seedling bank (Fig. 5.3).

Abundance by species in the seedling bank was calculated on a ha^{-1} basis and averaged across plots within sites. Although the seedling bank was measured after the outbreak, it reflected pre-outbreak composition because age data revealed only a small percentage of sampled trees recruited after the outbreak; and of these most were sprouting *P. tremuloides*. To facilitate analysis, reconstructed pre-outbreak overstory trees per hectare (TPHA) were plotted over seedling bank TPHA (Fig. 5.3). Overstory abundance of non-host species reflects the presence of biological legacies and potential seed sources post-disturbance.

To quantify timing of establishment by individual species we generated a frequency distribution of seedling bank recruitment by pooling age data into decadal classes of origin. Evaluating the distribution for consistent or episodic seedling bank recruitment revealed whether a species more typically exhibited chronic or pulse regeneration. Long, drawn-out establishment indicated availability for response to overstory disturbance at any time since the earliest decade of seedling establishment, whereas spikes in origin dates indicated rapid establishment of a large number of individuals i.e., a pulse, likely a

response triggered by rapid environmental change. Seedling bank tree-ring counts in our analysis were not cross-dated and are therefore conservative.

Composite species-specific height growth rates were estimated by pooling all measured seedling bank individuals and fitting linear models of height and age. Using the fitted equation, average potential growth rates were used to suggest the potential of each species to accede to the canopy. After preliminary inspection, *P. tremuloides* data were split into two groups: one associated with lava flow substrates and another representing an absence of a lava flow substrate. The lava flow substrate population is almost entirely from the Lava Cone site, which is surrounded in every direction by ~1.6 km of recent (1000 – 5000 yr) lava flows. Lava flows are composed of large blocky boulders of basalt, making ungulate access both currently and historically impossible. Therefore, lava flow populations represented natural exclosures that have never experienced ungulate browsing, in contrast to the other sites. To evaluate the possibility for *P. tremuloides* canopy accession, approximate browsing height thresholds were juxtaposed over height growth patterns. Height thresholds were: 200 cm for *Cervus elaphus* (elk) (Romme et al. 1995), 130 cm for *Odocoileus hemionus* (deer) and 115 cm for domestic *Ovis aries* (sheep) (Sampson 1923).

Biological legacies of the pre-outbreak forest were represented by remnant, live overstory trees which are a residual seed source, and by a seedling bank of advance regeneration. Relationships between these components were assessed to indicate potential scenarios of future forests and successional dynamics. To determine if pre-outbreak overstory composition influenced the seedling bank composition post-outbreak, three metrics were calculated for both the overstory and seedling bank.

1) Berger-Parker dominance (D)

$$D = N_{(MAX)} / N$$

where $N_{(MAX)}$ is the number of individuals in the largest group and N is the total number of individuals on a given plot.

2) Shannon diversity (H')

$$H' = \sum_{i=1}^n p_i \ln p_i$$

where p_i is the proportion of species i and \ln is the natural log.

3) Shannon Evenness (E_H),

$$E_H = H' / H_{(MAX)}$$

where H' is defined above, $H_{(MAX)}$ is maximum H' .

In order for metrics to be comparable between the overstory and the seedling bank each was calculated using estimated TPHA. Relationships were assessed by calculating Pearson correlation coefficients. Any predictable relationship could potentially yield important information regarding the hastening or delay of succession as a result of the *D. rufipennis* outbreak.

Results

It is likely *A. lasiocarpa* has been continuously establishing in the seedling bank for many centuries. We measured individuals with establishment dates to 1800 (age range 6 – 205 yr). A decreasing percentage of those individuals persisted through time because of the balance between establishment and mortality that occurs in the seedling bank when canopy accession is restricted (Fig. 5.4). *P. engelmannii* also likely had continuous establishment for centuries. We measured individuals as old as 152 yr, although *P.*

engelmannii never represented more than 1% of the seedling bank in any given decade (Fig. 5.4). Clearly both *A. lasiocarpa* and *P. engelmannii* were chronic regenerators prior to the *D. rufipennis* outbreak, although at drastically different levels (Fig. 5.4). *P. tremuloides* exhibited a pulse response immediately following the death of canopy *P. engelmannii* associated with the recent outbreak, which varied by year across the plateau but was manifest in the spikes of establishment seen in the 1990s and 2000s (Fig. 5.4). Although *P. tremuloides* ranged in age from 1 – 36 yr, the few individuals present during the 1970s and 1980s established under ungulate-free circumstances on lava substrates. The only other seedling bank species sampled were one *P. ponderosa* and three *P. pungens*; all at Mammoth Creek. The three *P. pungens* were recruited into the seedling bank in 1900 (1) and 1940 (2).

The chronically regenerating species *A. lasiocarpa* and *P. engelmannii* had similar height growth patterns of 1.2 cm per yr (Figs. 5.5 and 5.6); although, for *A. lasiocarpa* they were extremely variable and ranged from ~8 cm per yr to < 0.25 cm per yr. Average growth rate suggested that by the time ~ 2 – 3.5 m in height was reached the species were capable of accession to the overstory (threshold of 5 cm DBH used in this study); however seedling bank ages (Fig. 5.4) suggested canopy accession is a very rare event. The post-outbreak *P. tremuloides* (<20 yr) from two different populations, lava (non-browsed) and non-lava (browsed) have drastically different net height growth rates (Fig. 5.7). It is clear *P. tremuloides* from all sites without a lava substrate were unable to attain heights above the minimum browsing threshold, masking the expected pulse response to the high-severity *D. rufipennis* disturbance.

The outbreak resulted in ~96% mortality of overstory *P. engelmannii* (R.J. DeRose unpubl. data). Furthermore, almost none of the seedling bank established after the outbreak. As a result, the site-by-site comparison of pre-outbreak overstory TPHA and post-outbreak seedling bank TPHA highlights the drastic reduction in *P. engelmannii* site dominance as a result of the outbreak (Figs. 5.2 and 5.3). In some stands there were virtually no *P. engelmannii* in the seedling bank (e.g. Bristlecone Pine Trail, South Face) whereas in a few stands there was some *P. engelmannii* regeneration (e.g., Midway Face, North Hancock); however, there is a paucity of *P. engelmannii* across the 14 sites. In most cases *A. lasiocarpa* was well-represented in the overstory and abundant in the seedling bank. Indeed, the species composition of the seedling bank is almost certainly indicative of potential future dominance by *A. lasiocarpa* and to a lesser degree *P. tremuloides* (Fig. 5.3).

Comparisons of three metrics relating to composition revealed little relationship between pre-outbreak overstory and post-outbreak seedling bank composition. In all cases regressions of the metrics between overstory and seedling bank components showed no significant relationship ($\alpha = 0.05$ level) and there was little correlation among the metrics (Table 5.2). Only for *A. lasiocarpa* was there a relationship overall between overstory and seedling bank abundance ($R^2 = 0.41$, $P < 0.001$). Many plots contained only *A. lasiocarpa* i.e. $D = 1$ and for these plots $H' = 0$, which indicated complete dominance and no diversity, respectively. Similarly, there was no relationship in E_H between the overstory and the seedling bank.

Discussion

Our purpose in this study was to characterize regeneration response to a *D. rufipennis* outbreak and to describe its effects on stand dynamics. We also evaluate how it compared with the high-severity, infrequent / low-severity, frequent conceptualization of *P. engelmannii* - *A. lasiocarpa* disturbance regimes. We found the regeneration response to the outbreak did not fit the conceptual disturbance regime model. Instead, the host-specific, high-severity, infrequent *D. rufipennis* outbreak promoted a regeneration response dominated by the pre-existing seedling bank.

Had the recent high-severity disturbance been a stand-replacing fire instead of a host-specific beetle outbreak, most individuals in both the overstory and the seedling bank would have been killed, regardless of species, not just *P. engelmannii*. The resulting forest reorganization would have included a pulse of *P. tremuloides*, vigorously resprouting from root suckers on sites where root stocks were present prior to the fire. In many *P. engelmannii* - *A. lasiocarpa* forests *P. contorta* also responds favorably to stand-replacing fire; however, the Markagunt Plateau is outside the geographic range of this species. It is possible that mature, thick bark *P. menziesii*, and to a lesser extent *P. flexilis* would survive the fire in rare refugia, and be available as seed sources. Somewhat counterintuitively, it is possible that a stand-replacing fire would have been more advantageous for *P. engelmannii* recolonization, since post-fire there is a window of establishment possibility i.e., the ‘colonization phase’ prior to the *P. engelmannii* ‘exclusion phase’ (*sensu* Aplet et al. 1988) and it is likely fire is what initially regenerated at least some of the recently killed stands on the Markagunt Plateau (DeRose & Long 2007). In addition, a large-scale fire would have exposed mineral soil, necessary

for *P. engelmannii* establishment (e.g., see Kulakowski & Veblen 2006) and the seed source would have come from biological legacies on rocky outcrops, and in moist refugia. Finally, a stand-replacing fire would have killed most canopy and seedling bank *A. lasiocarpa*, a drastically different outcome than the recent *D. rufipennis* outbreak (Fig. 5.3). The result would be few *A. lasiocarpa* legacies and a possible lengthening of the time (decades) before *A. lasiocarpa* regenerated the burned site (Little et al. 1994).

Absent a high-severity disturbance, the Markagunt Plateau would eventually begin to have gap-forming disturbances, in which primarily mature trees, individually or in small groups, would be killed. The continuous creation of small patches would favor the chronic regeneration of shade-tolerant *P. engelmannii* and *A. lasiocarpa* in the seedling bank (Veblen 1986). Gaps with tip-up mounds, dead and down wood (Zielonka 2006), or mineral soil would favor *P. engelmannii* establishment, whereas gaps due to broken stems or crowns and thick litter layers would favor *A. lasiocarpa*. In the continued absence of a high-severity disturbance, the process of chronically regenerating species would have maintained a multi-aged *P. engelmannii* - *A. lasiocarpa* forest where species coexistence would be mediated by a balance between long-lived *P. engelmannii* and prolifically regenerating *A. lasiocarpa* (Veblen 1986; Aplet et al. 1988).

Regeneration response to some disturbance regimes does not necessarily fit the high-severity, infrequent / low-severity, frequent model. For example, mixed-severity disturbance regimes operate at different spatial and temporal scales. Fire regimes in Rocky Mountain *P. menziesii* forests create spatial heterogeneity of burned patches on the landscape (Klenner et al. 2008). Catastrophic wind and bark beetle outbreaks are disturbances that are more difficult to characterize with the conventional disturbance

regime conceptual model. Although high-severity and infrequent, they are both fundamentally different from stand-replacing fire. Like fire, severe wind storms are not fundamentally species-specific and create large patches of growing space (Foster & Boose 1992). However, wind storms mostly affect overstory individuals leaving biological legacies such as shade-tolerant, late seral species which have chronically established in the seedling bank and can persist in low light conditions until being released by canopy disturbance. Regeneration response to high-severity wind throw is likely a combination of new establishment of pulse species and a release of chronic species from the seedling bank (Cooper-Ellis et al. 1999; Kulakowski & Veblen 2003).

Unlike both catastrophic wind and stand-replacing fire, the high-severity *D. rufipennis* outbreak on the Markagunt Plateau resulted in beetle populations that selectively killed only overstory *P. engelmannii*, leaving the non-host overstory trees and the seedling bank to respond. Moreover, prior to the outbreak the canopy was heavily dominated by dense, mature (many centuries old) *P. engelmannii* with a sub-canopy of *A. lasiocarpa* (Fig. 5.2), so that when the outbreak killed the dominant *P. engelmannii* it left almost entirely *A. lasiocarpa* in both the overstory and seedling bank (Figs. 5.3 and 5.4). The dominance of *A. lasiocarpa* in both the overstory and seedling bank (in terms of TPHA) is likely the reason metrics of pre-outbreak overstory and post-outbreak seedling bank composition were unrelated (Table 5.2), not unlike that found by Lecomte et al. (2005). Overstory *P. engelmannii* were rare or completely absent from our sites post-outbreak, and since seed-bearing *P. engelmannii* exhibit irregular years of good seed production (Long 1994) and do not form a soil seed bank that persists longer than nine months (Greene et al. 1999), seed from *P. engelmannii* will not effectively contribute to the future forest. Overstory

biological legacies of species other than *A. lasiocarpa*, such as *P. tremuloides* and, less commonly, *P. menziesii* and *P. flexilis* occurred on the plateau (Fig. 5.3); however, they were rare and unlikely to effectively contribute to regeneration response. In Canada, Astrup et al. (2008) found little evidence for a post-*Dendroctonus ponderosae* outbreak pulse of regeneration, like would be expected after fire, and instead concluded that response was likely dominated by previously established individuals (advance regeneration) composed almost entirely of *A. lasiocarpa*. In contrast to our data and Astrup et al. (2008), Axelson et al. (2009) found *D. ponderosae* -affected *P. contorta* forests had adequate representation of live *P. contorta* in the canopy (29%) and sub-canopy (25%) post-outbreak that would contribute to forest reorganization.

A regeneration response to the recent outbreak characteristic of low-severity, frequent disturbance was evident in our data. The process of chronic seedling bank regeneration has likely been occurring for centuries (Fig. 5.4); however, it was much more pronounced for *A. lasiocarpa* than for *P. engelmannii*, which is consistent with their relative shade-tolerances (Kobe & Coates 1997). Moreover, the large difference in numbers between these two species suggested *A. lasiocarpa* was better able to establish in the thick litter associated with this *P. engelmannii* - *A. lasiocarpa* forest floor (Noble & Alexander 1977) and likely relied on a long-lived seedling bank to maintain its position as a sub-canopy associate of *P. engelmannii* (Veblen 1986; Antos & Parish 2002). In contrast, *P. engelmannii* has more exacting seedbed requirements and, as reflected in our data, only rarely establishes, probably when an appropriate microsite becomes available. Indeed, *P. engelmannii* regeneration has been found to be limited to sites with thin to no litter layer (Noble & Alexander 1977; Knapp & Smith 1982). The bell-shaped age frequency

distribution of the chronic regenerators was likely a result of the gradual mortality of most of the seedling bank over time, suggesting they can not survive indefinitely (Fig. 5.4). However, our data were not inconsistent with the observation by Veblen et al. (1991a) of an overall increase of seedling bank *A. lasiocarpa* in general in *P. engelmannii* - *A. lasiocarpa* communities of Rocky Mountain National Park during the last 100 yrs, possibly a result of increased regional moisture.

In contrast to a *D. rufipennis* outbreak, disturbances that expose mineral soil increase the likelihood of *P. engelmannii* establishment. Canopy gaps in old-growth forests as a result of low-severity, gap-phase dynamics create and maintain the necessary seedbed conditions (i.e. fallen logs, tip-up mounds, and mineral soil) for *P. engelmannii* establishment and also allow it to increase its representation in the seedling bank (Kulakowski & Veblen 2003). There was limited evidence of pit and mound topography on our sites (R.J. DeRose, in preparation), which may partially explain the very low numbers of *P. engelmannii* in the seedling bank. Relatively low abundances of *P. engelmannii* have been found in other systems, e.g., Schulze et al. (2005) suggested seedling bank density of *Picea obovata* in the Dark Taiga forest ranged from 100 – 400 TPHA but did not state over what time period these trees established. Similarly, Antos and Parish (2002) found 7.6% of the *P. engelmannii* - *A. lasiocarpa* forest seedling bank was *P. engelmannii* in British Columbia. If we assume the ~ 1% establishment of *P. engelmannii* per decade on our sites in the mid- to late-1900s (from Fig. 5.4) represented average decadal recruitment into the seedling bank, then ~ 50 seedlings ha⁻¹ yr⁻¹ became established, whereas the ~ 10% establishment, on average, of *A. lasiocarpa* over the same time period translated into ~ 550 seedlings ha⁻¹ yr⁻¹. Therefore, although *A. lasiocarpa*

exhibits a more rapid extinction in numbers over time than *P. engelmannii* (from right to left on Fig. 5.4), it maintained much larger quantities in the seedling bank overall.

Furthermore, although overall seedling bank abundances appeared high enough to be adequate for forest regeneration (Fig. 5.3, *sensu* Nigh et al. (2008), in beetle-killed *P. contorta*), *A. lasiocarpa* makes up a vast majority of that total. Antos et al. (2000) suggested the paucity of *P. engelmannii* observed on two sites in British Columbia is partially offset by its' increased height growth; however, we found no height growth advantage for *P. engelmannii* in our data (Figs. 5.5 and 5.6).

In contrast to *A. lasiocarpa* and *P. engelmannii*, the regeneration response of *P. tremuloides* was a characteristic pulse, as expected given the high-severity 1990s beetle outbreak (Fig. 5.4). Nevertheless, with the exception of sites with a lava flow substrate (i.e. Lava Cone and Mammoth Creek) virtually none of the *P. tremuloides* pulse achieved heights above the minimum browsing threshold (Fig. 5.7). *P. tremuloides* on lava flow substrates reflect height growth in the absence of browsing, whereas the balance of *P. tremuloides* on the plateau are simply unlikely to attain appropriate height for canopy accession due to browsing pressure from both domestic and native ungulates. *Odocoileus hemionus* (deer), *Cervus elaphus* (elk), *Ovis aries* (domestic sheep), and *Bos* spp. (domestic cattle) are primarily responsible for browsing pressure on the Markagunt Plateau. In general, *O. aries* browse choice is similar to *O. hemionus*, with a preference for leaves and tender stems, whereas *C. elaphus* eat a more varied diet. As a result, *O. aries* browsing should directly increase the grass component by removing the herbaceous component which the *C. elaphus* prefer; however, if there are too many *O. aries*, *C. elaphus* might have to find something else to eat (i.e., *P. tremuloides*; Sampson 1923). In

addition to *O. aries*, if *Bos* spp. are present they will compete with the *C. elaphus* for grass, further pushing the *C. elaphus* to rely on *P. tremuloides*. Indeed, recent work has found evidence of top-down regulation of *P. tremuloides* by *C. elaphus* in Yellowstone National Park (Halofsky & Ripple 2008) where increased *P. tremuloides* growth has resulted from the coupling of recent fire and reduced *C. elaphus* herbivory, presumably from increased *Canis lupus* (wolf) presence (Halofsky et al. 2008).

In sharp contrast to other large-scale, high-severity disturbance types such as fire, the recent *D. rufipennis* outbreak did not destroy the non-host overstory or seedling bank, nor did it create environmental conditions generally associated with pulse regeneration of early seral species as we would expect given the conventional disturbance regime conceptualization. Instead, the loss of the dominant overstory *P. engelmannii* has opened growing space for the few non-host overstory species, where they occur, and released the seedling bank of primarily *A. lasiocarpa*, which has been chronically regenerating for centuries. Although *P. tremuloides* exhibited a pulse regeneration response to the outbreak it will not dominate post-outbreak stands (except on lava substrates) because of intense browsing pressure. In this once *P. engelmannii*-dominated landscape, the relatively few residual, non-host overstory trees will not be able to fully reoccupy the growing space; instead, the seedling bank will play the primary role in regeneration response. The chronically regenerating seedling bank, typically associated with canopy gaps, created by low-severity disturbances, is posed to dominate forest reorganization in response to the high-severity, host-specific *D. rufipennis* outbreak.

The regeneration response to this high-severity, host-specific outbreak may not be typical of what has happened previously on our site. However, such atypical regeneration

response in western North America might become more common in the future due to changing bark beetle dynamics. Beetle outbreaks, both *D. rufipennis* on the Kenai Peninsula of Alaska (Berg et al. 2006), and *D. ponderosae* in western Canada (Wulder et al. 2006), and northern Colorado (D. Kulakowski & T.T. Veblen, unpubl. report) are affecting larger areas than previously documented. Increasing area of susceptible hosts, predicted shifts in *D. rufipennis* populations from one generation every two year to one generation in a single year (Bentz et al., submitted), and a predicted shift in *P. engelmannii* habitat to higher elevations (Rehfeldt et al. 2006) may all contribute to altered disturbance dynamics of *P. engelmannii* and a reduction in area of *P. engelmannii* forest in the western U.S.

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Table 5.1. Site and seedling bank attributes for the sampled stands

Site	No. plots	Elevation range (m asl)	Slope (%)	Aspect	Seedling bank density / m ²			
					<i>Abies lasiocarpa</i>	<i>Populus tremuloides</i>	<i>Picea engelmannii</i>	Other*
Ashdown	9	3176-3219	0-5	North	1.48	-	0.03	-
Bristlecone Pine Trail	4	2974-3038	15-40	Northwest	0.16	-	-	-
North Hancock	10	3054-3127	3-30	North	2.55	-	0.37	-
Hancock Peak Trail	10	3062-3101	0-5	Southeast	0.70	1.31	0.06	-
Lava Cone	10	2926-3032	0-20	Variable	1.00	0.29	0.03	-
Lava Flow	3	3125-3147	5-10	Southwest	4.44	0.44	0.11	-
Midway Face	3	2980-3172	5-10	North	1.56	2.33	0.56	-
Midway Point	10	2931-2988	0-3	North	2.33	0.71	0.08	-
Mammoth Creek	10	2618-2723	15-40	North	0.16	0.16	0.02	<0.001
Navajo Lake	10	2845-2914	10-30	Northeast	0.24	0.03	0.02	-
Rainbow Meadow	5	3179-3233	2-10	South	3.07	0.43	0.10	-
Snotel	10	3154-3250	5-45	North	0.21	-	0.02	-
South Face	3	2990-2993	15-30	South	2.00	1.11	-	-
Sydney Valley	10	3073-3117	3-15	Southwest	4.48	0.13	0.08	-
Averages:					1.74	0.50	0.11	<0.001

* Other: 1 – *Pinus ponderosa*, 3 – *Picea pungens*.

Table 5.2. Correlation coefficients for overstory and seedling bank diversity metrics

		Overstory			Seedling bank		
		D	H'	E_H	D	H'	E_H
Overstory	D	1.0					
	H'	-0.95	1.0				
	E_H	-0.84	0.81	1.0			
Seedling bank	D	0.13	-0.16	-0.07	1.0		
	H'	-0.10	0.12	-0.04	-0.94	1.0	
	E_H	0.12	-0.13	0.05	-0.90	0.96	1.0

Note: D – Berger-Parker dominance, H' – Shannon diversity, E_H – Shannon evenness.

Grey area indicates correlations between overstory and seedling bank.

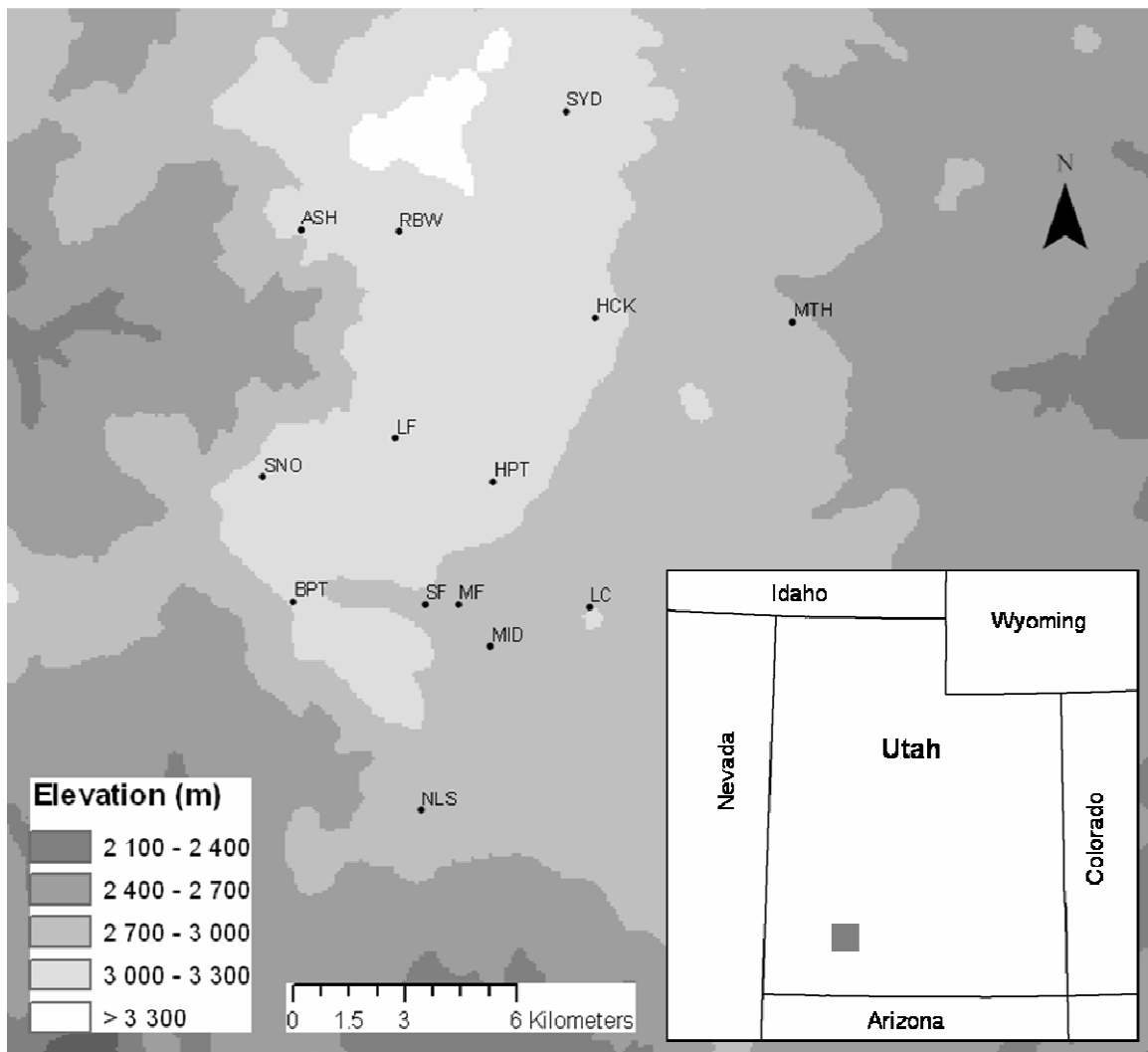


Fig. 5.1. Map of the Markagunt Plateau showing location of study sites. Study site labels are as follows (see Table 1): ASH – Ashdown, BPT – Bristlecone Pine Trail, HCK – North Hancock, HPT – Hancock Peak Trail, LC – Lava Cone, LF – Lava Flow, MF – Midway Face, MID – Midway Point, MTH – Mammoth Creek, NLS – Navajo Lake, RBW – Rainbow Meadows, SNO – Snotel, SF – South Face, SYD, Sydney Valley.

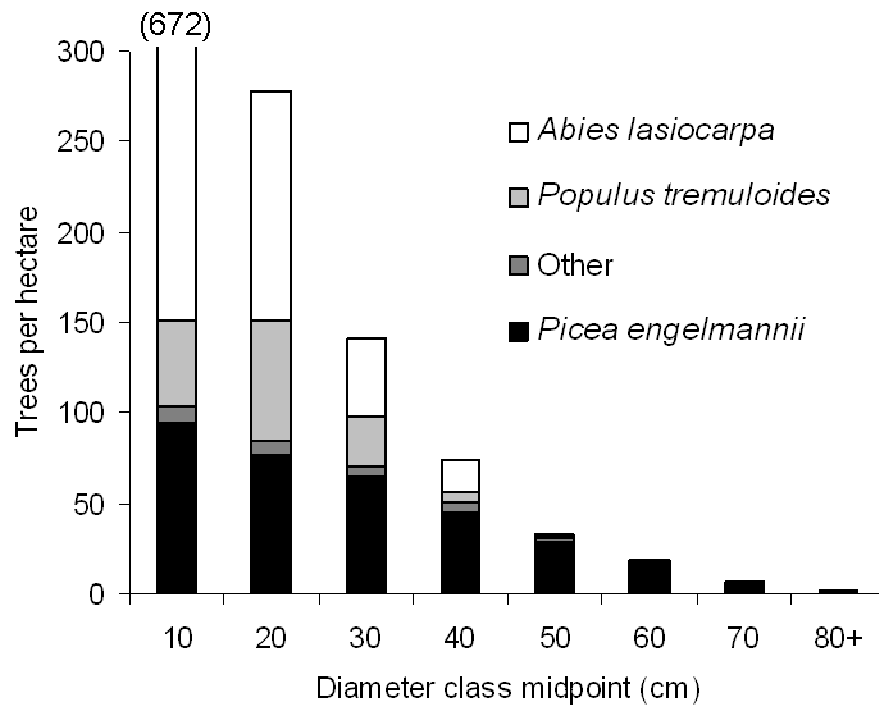


Fig. 5.2. Composite diameter distribution for all 14 sites constructed from pre-outbreak live overstory (>5 cm DBH) trees per hectare by 10 cm diameter class showing dominance by *Picea engelmannii*. The 80+ category includes *Picea engelmannii* up to 130 cm. Other includes, in order of abundance: *Pseudotsuga menziesii*, *Pinus flexilis*, *Pinus ponderosa*, *Picea pungens*, *Abies concolor*.

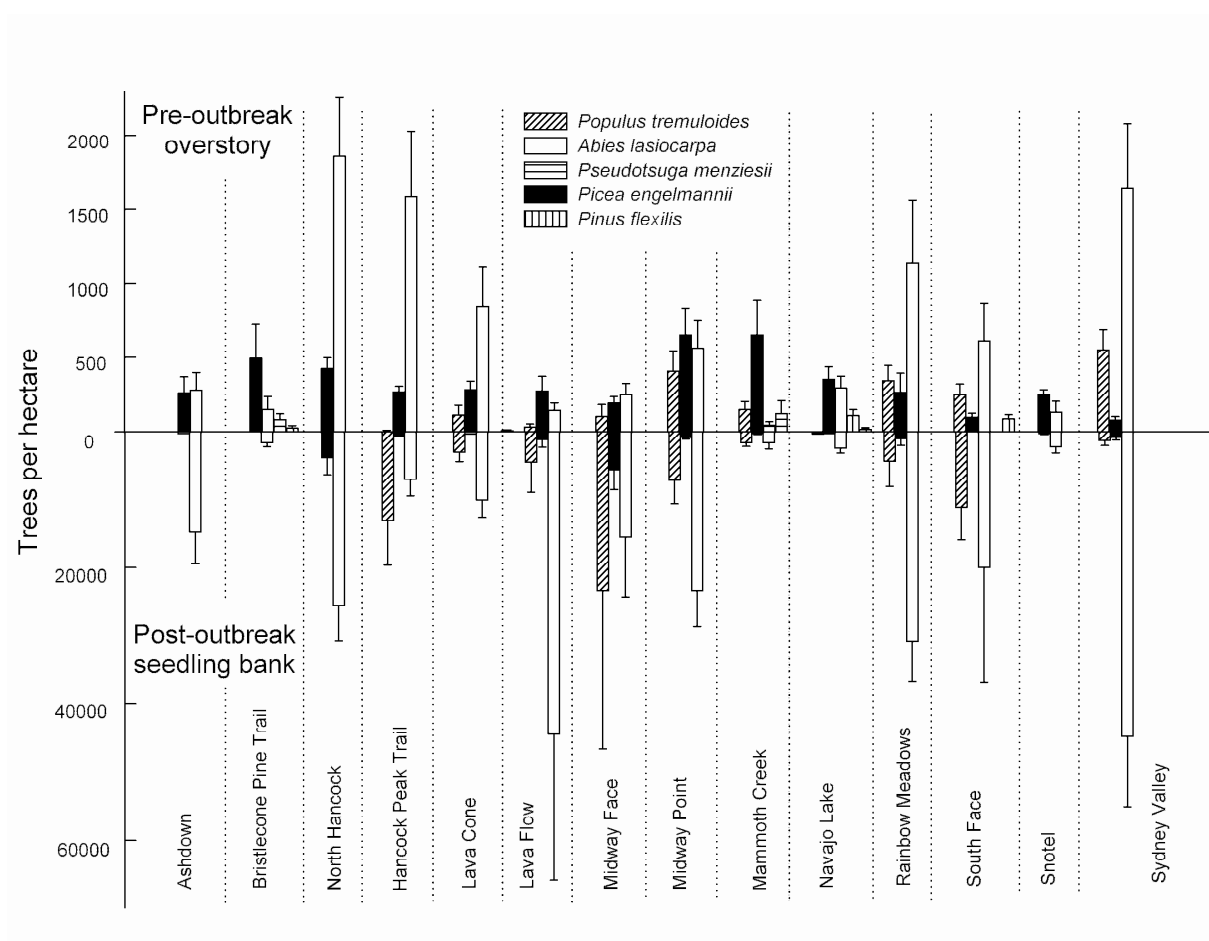


Fig. 5.3. Pre-outbreak overstory trees per hectare, averaged per site, reconstructed from field data plotted over post-outbreak seedling bank trees per hectare by species shows: 1) the paucity of *Picea engelmannii* in the seedling bank, 2) remaining overstory species after the host-specific beetle outbreak. Individual sites are named and divided by dotted lines (see Table 5.1).

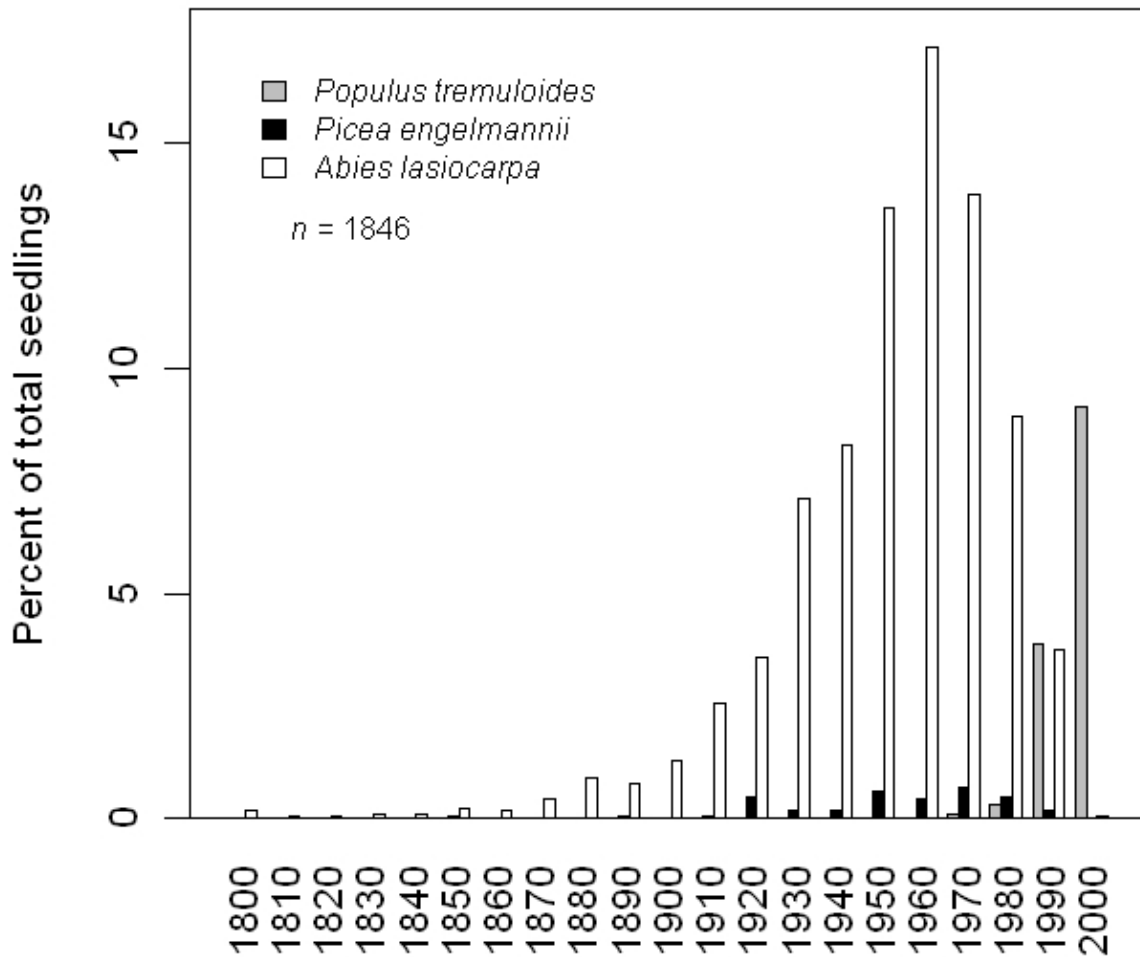


Fig. 5.4. Frequency distribution (percent of total seedlings) of decade of establishment by species for the seedling bank. Chronic regeneration of *Abies lasiocarpa* dated to 1800. *Picea engelmannii* establishment dated to 1850, but was chronically occurring from 1910-2000. A pulse of *Populus tremuloides* establishment occurred in 1990 and 2000. *Picea pungens* was recruited once in 1900 and twice in 1940 (not shown in legend).

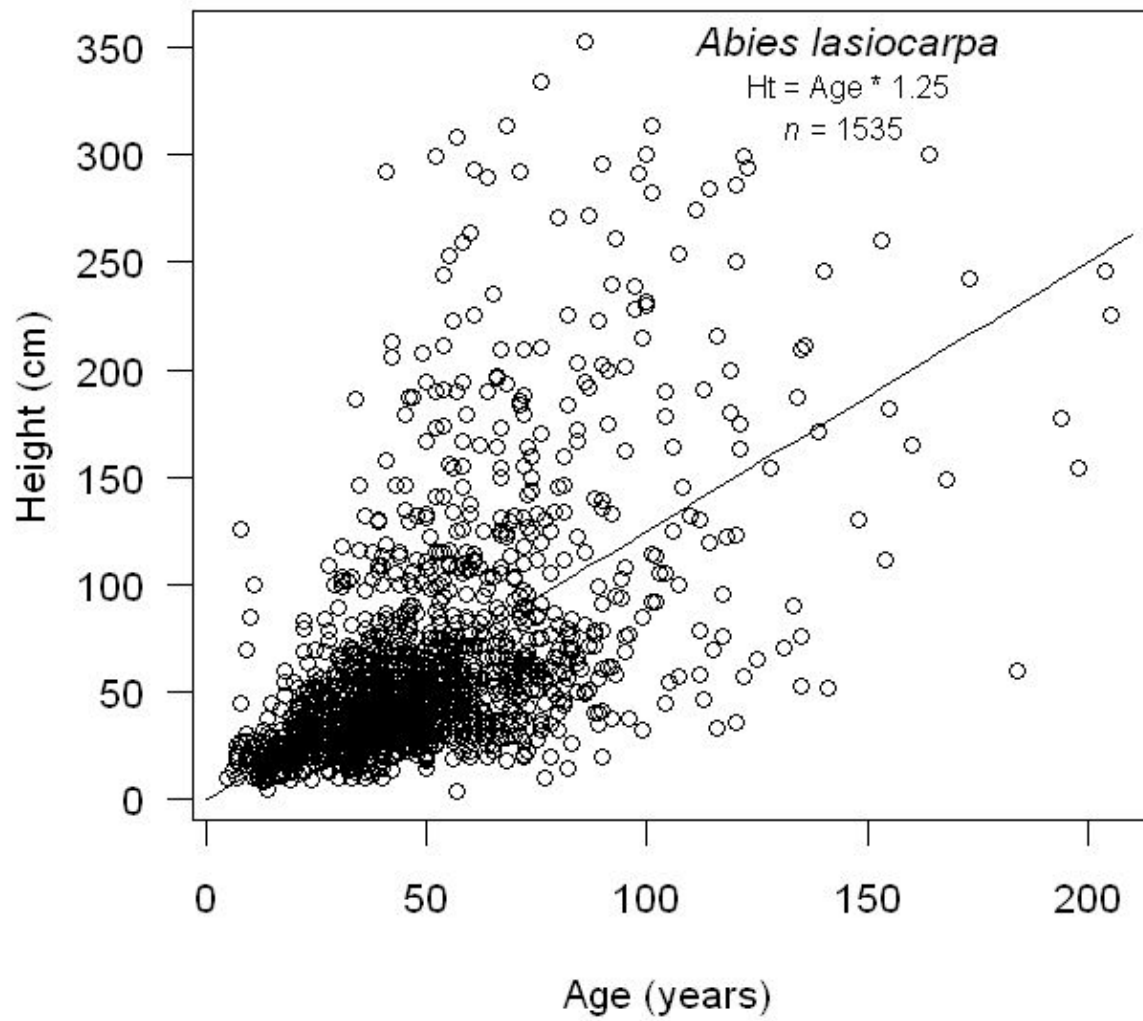


Fig. 5.5. Height (cm) – age (yr) relationship for *Abies lasiocarpa*. Data pooled across all sites.

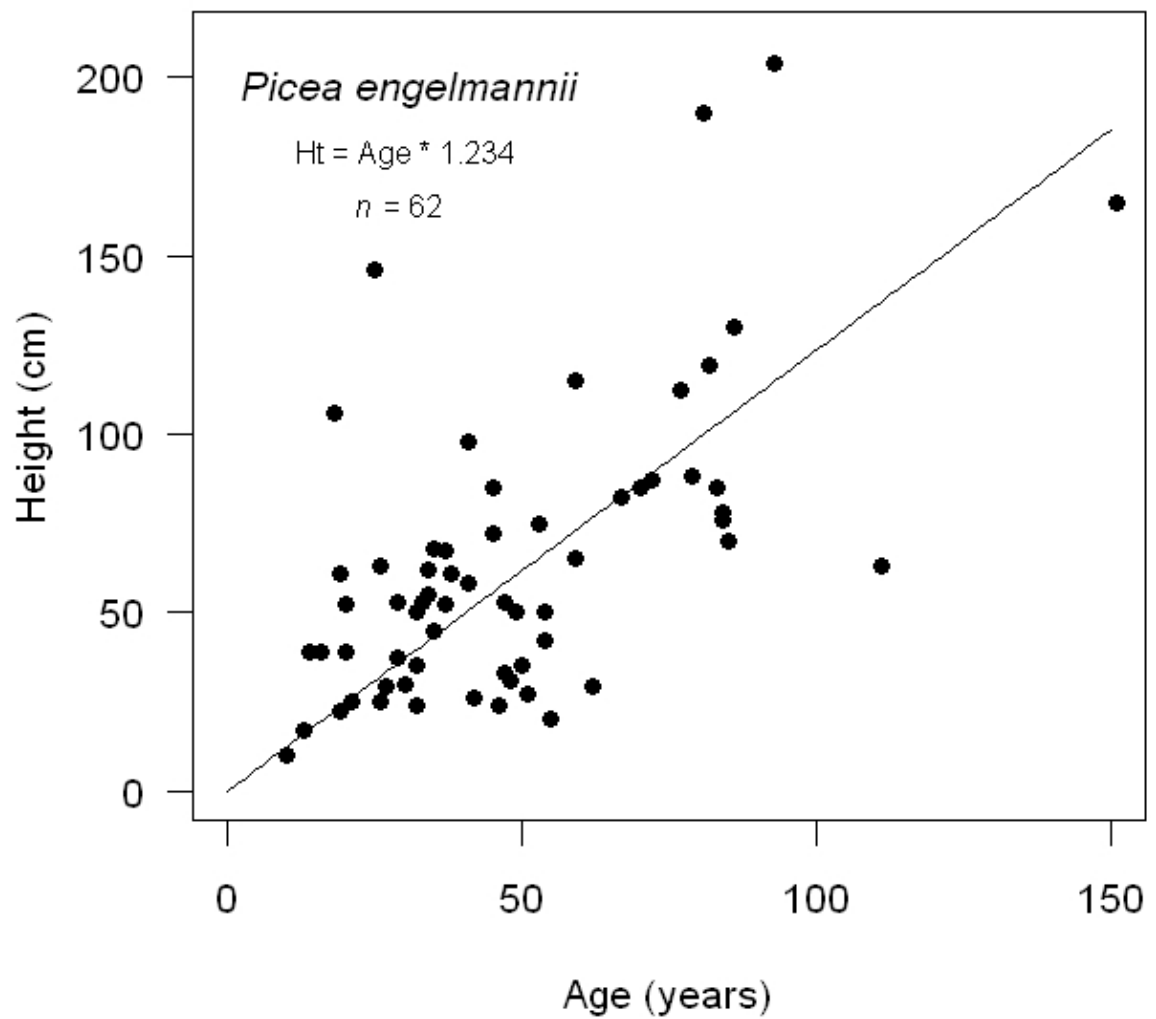


Fig. 5.6. Height (cm) – age (yr) relationship for *Picea engelmannii*. Data pooled across all sites.

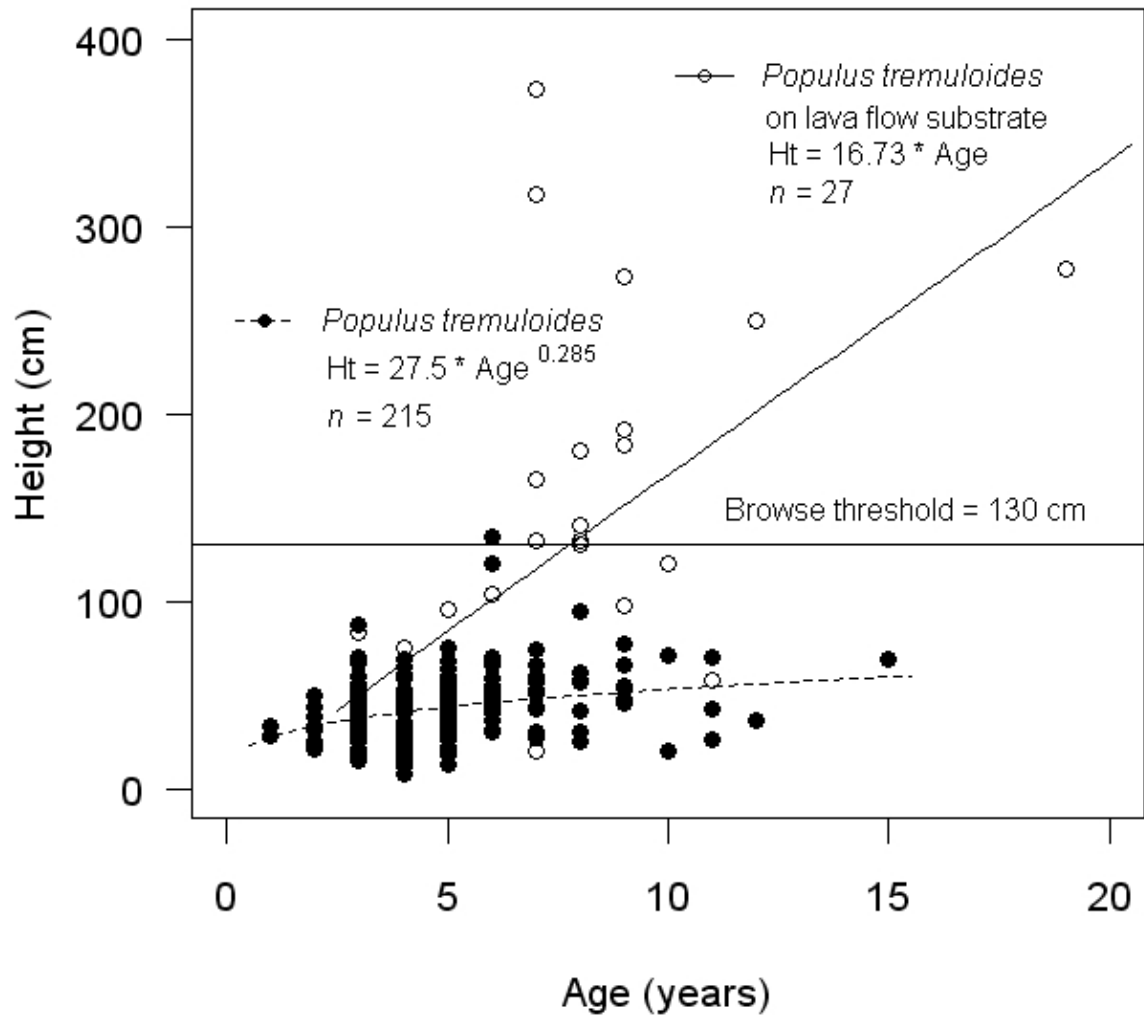


Fig. 5.7. Height (cm) – age (yr) relationships for post-outbreak (< 20 yr) *Populus tremuloides* across the Markagunt Plateau. Aspen height growth rate calculated separately for sites with (absence of lava flow) and without (lava flow substrate) browsing pressure, to show the potential difference due to grazing history. See text for explanation. Regression lines plotted to suggest average height growth rates.

CHAPTER 6

SILVICULTURAL CONSIDERATIONS FOR RESISTANCE AND RESILIENC OF
ENGELMANN SPRUCE FORESTS TO SPRUCE BEETLE OUTBREAKS IN THE
INTERMOUNTAIN WEST ⁹

Abstract

In western North America widespread mortality as a result of bark beetle outbreaks has increased in both severity and extent. In the Intermountain West unprecedented spruce beetle (*Dendroctonus rufipennis*) outbreaks have occurred during the last 20 yrs. Given the limited management options that have been studied for Engelmann spruce (*Picea engelmannii*) forests, silviculturists are questioning what they can do to limit the loss from likely inevitable spruce beetle outbreaks. Directly managing beetle populations is intensive, expensive and has limited applicability; therefore, we examine alternatives for indirectly managing beetle habitat using the concepts of resistance and resilience. Resistance can be thought of as related to spruce beetle response to vegetation characteristics, or the inability of spruce beetle populations to build as a result of forest structure and composition. Resistant stands, for example, might have a high percentage of non-host species, low relative densities, or small host size. Resistant landscapes might be largely dominated by young, vigorous stands of spruce or stands dominated by non-host tree species. In contrast, resilience can be thought of as the vegetation response to spruce beetle populations at outbreak levels, and its attributes depend on management goals. We suggest compositional and structural changes are appropriate to describe vegetation

⁹ Coauthored by R. Justin DeRose and James N. Long

response to beetle outbreaks, and therefore resilient stands would maintain: mature forest character, mature spruce, or potential for future spruce dominance. Resilient landscapes would have spruce age class diversity and a low percentage of host species in spatially discontinuous patches.

Introduction

In the last few decades bark beetle outbreaks have been increasing in extent and severity across western North America (Logan and Powell 2001, Berg et al. 2006, Wulder et al. 2006). In the southern Rocky Mountains of Utah, recent spruce beetle (*Dendroctonus rufipennis*) outbreaks in Engelmann spruce (*Picea engelmannii*) forests (Dymerski et al. 2001, DeRose and Long 2007) dwarfed the spatial extent and severity of known, historical outbreaks (Mielke 1950, Schmid and Frye 1977). For example, an unprecedented outbreak on the Markagunt Plateau in southwestern Utah resulted in landscape-wide mortality of virtually all mature spruce (DeRose and Long 2007). Furthermore, virtually no young spruce stands or advance regeneration exist across the plateau (see Chapter 5). The potential for this sort of outbreak in Engelmann spruce forests has silviculturists questioning how and even whether they can do anything to reduce loss from the spruce beetle. What are the silvicultural options in the face of increasing bark beetle pressure? What, if anything, could be done to head off an outbreak? Can we build resistance or resilience?

We provide an overview of (1) spruce beetle population dynamics, (2) the silvicultural toolkit for dealing with spruce beetles, (3) what resistance and resilience mean in the

context of host-beetle interactions, and, (4) suggestions for circumstances where silvicultural intervention might be useful.

Spruce beetle population dynamics

Three things are necessary for spruce beetle populations to transition from endemic to incipient, and finally to epidemic (outbreak): presence of spruce beetles, amenable weather, and suitable habitat. Spruce beetle populations normally exist in low numbers (endemic) in spruce forests and, over time in the absence of other disturbances (e.g., fire), it is likely that conditions (e.g., dense, mature stands of spruce) for increasing beetle populations will eventually occur resulting in infrequent, landscape-extent outbreaks (epidemics). When a catalyst such as downed trees that result from avalanches, wind throw, or logging (Schmid 1981) facilitates population growth, an endemic-to-incipient threshold can be crossed. Once at the incipient level, it is thought that, given sufficient host and amenable environmental conditions, an incipient-to-epidemic shift is likely when thresholds associated with multiple factors, including temperature and host tree resistance, have been crossed (Raffa et al. 2008). Some of these factors are, of course, beyond the control of silviculturists (e.g., temperature), but we can potentially influence the beetles directly by aggressive sanitation, or indirectly by manipulating their habitat (e.g., forest structure and composition).

Silvicultural goals

Assuming that a management goal for Engelmann spruce forests in the face of spruce beetle pressure is to maintain spruce-dominated stands over the long-term, the primary management approach would likely involve efforts to build resistance and/or resilience.

Resistance is the ability of the system to withstand change caused by a disturbance whereas resilience is the ability of the system to respond to disturbance without fundamental change. Resistance promotes a high percentage of non-host species at low relative densities and small sizes whereas resilience promotes long-term age class and tree species diversity across the landscape. To evaluate these objectives measurable evaluation criteria are needed; for resistance a large percentage of the landscape should be dominated by young, vigorous stands of spruce, and for resilience the landscape should have a low percentage of host species and spruce age class diversity in spatially discontinuous patches. In the absence of spruce, maintaining forest character while actively working to incorporate spruce back into the system is a desirable approach. To meet these objectives, we describe direct and indirect silvicultural options, which differ primarily based on their focus; direct control manages the beetle whereas indirect control manages the beetle's habitat. We emphasize the latter when describing how to build resistance and resilience.

Using direct control

Directly managing beetle populations is done through stand treatments when the beetle population is at endemic levels. Pheromone traps, aerial spraying, trap-trees, and selective harvest of infested trees are approaches which directly target spruce beetle populations (Massey and Wygant 1954, Bentz and Munson 2000). Pheromone traps are deployed in the vicinity of known spruce beetle activity, but not in the host type, to decoy beetles from green host trees. The use of traps within the host type could result in green tree attack by the beetle. Aerial spraying involves the direct application of specific

insecticides to the tree bole up to a height of ~ 12 m (see Fettig et al. 2006 for details). Due to cost, spraying is only done on the most highly valued trees (e.g., campgrounds or roadsides) and therefore has very limited applicability over large landscapes. The trap tree approach involves felling green, susceptible hosts prior to peak beetle flight to attract spruce beetles, because prostrate trees attract ~10 times the numbers of beetles as standing trees (Nagel et al. 1957). The trap trees are subsequently burned or de-barked on-site or removed from the site. Sanitation, the removal or on-site treatment of infested trees, is another method to potentially reduce spruce beetle populations. Given the intensity of monitoring, treatment, and removal, both the trap tree and sanitation approaches require many resources and coordinated efforts (Bentz and Munson 2000). Furthermore, to influence phenomena that occur on the landscape like spruce beetle outbreaks, direct control would be intensive in terms of time, space and cost and therefore has limited applicability.

An example where virtually unlimited resources have been used can be found in Canada where the Albertan government has already spent over 250 million (Canadian currency) to directly control mountain pine beetle infestations before they cross into novel territory (i.e., boreal jack pine (*Pinus banksiana*) forests). Their plan has the monetary and political backing to actively monitor, treat, and remove infested lodgepole pine across the province¹⁰. This type of management is clearly not feasible for most forestland in North America.

Therefore, although directly managing the beetle populations has intuitive appeal, it is too costly to implement. Cost limitations due to the spatial and temporal extent of such

¹⁰ URL: http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/actionplan/2006/Beetle_Action_Plan.pdf

intensive ‘beetle-chasing’ treatments make direct control for spruce beetle outbreaks largely impractical. In contrast, indirect control of spruce beetle populations through habitat manipulation, i.e., building resistance and resilience, can be applied strategically to at-risk areas across a landscape to potentially head-off or mitigate, respectively, likely beetle outbreaks.

Building resistance

In Engelmann spruce forests, resistance results from those characteristics that limit beetle population change from one level to another and can be characterized as how the spruce beetle population responds to vegetation characteristics, i.e., the inability of spruce beetle populations to build as a result of forest structure and composition (Table 6.1). Stand-by-stand, resistance is low risk of increasing beetle populations from within the stand and can result from a high percentage of non-host species, low relative density and/or high spruce vigor (young stands of small trees), all of which make it difficult for beetle populations to increase (Table 6.2). Conventional ‘beetle-proofing’ management such as intermediate thinning modifies stand composition and increases individual tree vigor, thereby changing stand structure and altering the microclimate, making beetle mass-attack more difficult. For example, spacing has been suggested to control the transition from endemic to incipient in mountain pine beetle populations (Whitehead et al. 2006), although this has not been tested for the spruce beetle. However, control methods are small spatial extent (stand), short-term (i.e., 10-20 years) approaches that only ‘buy time’ before conditions again become conducive for beetle population growth. Maintaining stand resistance would require repeated entries to increase spruce vigor that

would remove non-host species and ultimately result in very large spruce, which are most susceptible to spruce beetle. As a result, judiciously providing resistance to spruce beetle outbreaks may actually contribute to an increase in susceptibility in the long-term. Furthermore, it is unlikely any stand activity will ultimately ‘resist’ a spruce beetle outbreak originating from outside the stand.

Anecdotal evidence from an Engelmann spruce thinning treatment on the Markagunt Plateau illustrates this point. The thinned stand resisted the mass-attack longer than the surrounding forest, but the effect lasted approximately one year before the resistant stand was overwhelmed by very high beetle population levels (P. Eisenhauer, personal communication). Therefore, thinning to provide resistance to the spruce beetle is realistically only a stand tool to limit endemic populations and, if used, should be carefully considered in the context of adjacent stands of susceptible host and beetle population levels.

At landscape extents, resistance is a low probability that beetle populations will build to outbreak levels (Table 6.1). For example, if a large percentage of the landscape was young it would be resistant (Table 6.2), but only in the short-term. Only in special situations would managing for short-term resistance on the landscape be practical, e.g., when the landscape is small and isolated such as high elevation ‘islands’ of Engelmann spruce forest that occur within the larger forested landscape dominated by non-host species in the Rocky Mountains. The relatively small size of these islands makes intensive management potentially practical. As an example of such isolated spruce forests, the T.W. Daniel Experimental Forest is a relatively small (250 ha) island of Engelmann spruce forest in the Bear River Mountains of northern Utah. Experimental

and operational treatments have been conducted that were designed to reduce stand density, improve residual tree vigor, and regenerate spruce (Figure 6.1), all desirable management actions to resist a beetle outbreak by modifying composition and structure. In addition, direct control of endemic beetle populations in the form of trap trees and sanitation was done (Bentz and Munson 2000), which has so far been successful. The combination of these activities has the potential to deter a beetle outbreak in the short-term. However, in the long-term, as trees and stands age, maintaining landscape resistance would become increasingly difficult, and the landscape will become increasingly susceptible to beetle outbreaks.

The idea that we have limited ability to affect spruce beetle outbreaks is fundamentally different than how we think about fuels reduction treatments to directly influence crown fire behavior. Stand fuel reduction treatments have been shown to increase resistance to fire by creating patches where active crown fire is knocked down to the surface resulting in reduced mortality (Strom and Fule 2007). Furthermore, strategically placed fuel reduction treatments can, at least in theory, slow fire spread by as much as 60% with as little as 20% of the area treated (Finney 2001). In theory, this strategy might work to slow the spread of beetle outbreaks but no data are available concerning what percentage of the landscape would need to be treated; however, we suspect it would be very large, e.g., at least 70%, 80%, 90% (or more?). Like the fuels treatments above, it should be clear that stand treatments for resistance have ephemeral effects.

Building resilience

Resilience is the ability of the forest to respond to disturbance without fundamental and lasting change. Resilience can be thought of as the vegetation response to spruce beetle populations at outbreak levels. Attributes of resilience must be characterized in the context of management goals and objectives (see above), e.g., is the goal to maintain mature spruce or perhaps simply mature forest character after an outbreak? We suggest three indicators of forest composition and structure to describe potential vegetation response to spruce beetle outbreaks: (1) maintenance of mature stands, (2) maintenance of at least some mature spruce, and (3) maintenance of potential for spruce dominated forests in the long-term, represented by abundant young spruce (Table 6.1).

In Engelmann spruce forests, stand resilience that (1) maintains mature stand character or (2) maintains mature spruce, is associated with a low percentage of spruce (Tables 6.1 and 6.2). For example, stands on the Markagunt Plateau with a higher percentage of non-host species (e.g., subalpine fir) still had large living trees after the outbreak (DeRose and Long 2007). Similarly, stands that had been treated with partial cutting prior to spruce beetle activity had a higher proportion of post-outbreak spruce basal area (Hansen et al. 2009). Silvicultural activities which retain or increase the percentage of non-host species will build resilience so that a stand might absorb the disturbance without fundamental change from its basic stand structure, ensuring maintenance of mature forest character in both the short- and long-term. Similarly, silvicultural activities which increase the percentage of non-host species, especially in stands with large diameter, can potentially mitigate beetle-caused mortality. On the Markagunt Plateau, the very few large

Engelmann spruce which survived the outbreak were in stands with relatively high percentages of non-host trees (DeRose and Long 2007).

Stand resilience that (3) maintains the potential for future spruce dominance in the face of a spruce beetle outbreak is associated with the presence of abundant young spruce (Tables 6.1 and 6.2) and can result from at least two conditions: (a) young spruce stands (i.e., less than 70 yrs, *sensu* Veblen et al. (1994)), or (b) stands with abundant spruce advance regeneration. For example, there were no young stands on the Markagunt Plateau prior to the outbreak (Figure 6.2) where spruce beetle-caused mortality ranged from 87 – 100% in stands that ranged in age from 225 – 512 years. In addition, advance regeneration was virtually absent beneath the mature stands prior to the outbreak (see Chapter 5). Furthermore, recently regenerated spruce stands (i.e., less than 70 years old) were lacking on the forest. Had young stands been present they would represent potential for mature spruce in the future.

To effectively promote Engelmann spruce establishment silvicultural intervention would need to be conducted well in advance of an outbreak. High-risk stands are excellent candidates for regeneration harvesting and can be identified using the spruce beetle risk rating system (Schmid and Frye 1976). These harvests should leave large, seed-bearing spruce when reducing stand density so that a ‘catch’ of spruce can become established (Figure 6.1). Group selection methods are conventionally used to regenerate spruce in the Rocky Mountains (Alexander 1987); however, consider using the shelterwood regeneration method because it can quickly and effectively create the microsite conditions (shade and mineral soil) necessary for timely spruce establishment (Figure 1), resulting in a young spruce stand that should not be susceptible for at least 70

years. Furthermore, the group selection method might regenerate 20% or less of an area in the first cutting cycle whereas the shelterwood method would regenerate the entire stand. Regardless of treatment, any regeneration is dependent on sufficient spruce seed trees (Goodman and Hungate 2006), or aggressive planting (see below).

Resilience on the landscape can be increased by creating and maintaining tree species diversity and spruce age class diversity across the forest (Table 6.2). When challenged by an outbreak both mature forest character and spruce-dominated stands should remain (Table 6.1). In Engelmann spruce landscapes with little or no age class diversity, i.e., homogeneity of mature spruce, we suggest the implementation of an aggressive program of (see above) regeneration harvests in stands across the landscape with the highest priority given to stands with the highest spruce beetle risk ratings. By increasing the representation of stands of young spruce (age class diversity) and increasing the heterogeneity of tree species diversity one can build both short- and long-term resilience.

Discussion

What happened on the Markagunt Plateau?

The Markagunt Plateau was not resistant to the spruce beetle outbreak because it had a low percentage of non-host-dominated stands, a high percentage of stands with high relative densities, and a high percentage of large spruce. This resulted in a large portion of the landscape being highly susceptible to an outbreak because there was a very low percentage of resistant stands (Table 6.2). Similarly, the Markagunt Plateau was not resilient after the outbreak because it had a high percentage of spruce stands, i.e., it was strongly dominated by Engelmann spruce, and had a paucity of young spruce: very few

recently regenerated or young stands, and virtually no advance regeneration (see Chapter 5). Therefore the pre-outbreak forest across the landscape had little spruce age class diversity and limited tree species diversity. Interestingly, thinning treatments on Midway Face of the Markagunt Plateau were conducted in 1998 to increase resistance to spruce beetle populations. Although these stands ultimately succumbed to epidemic beetle pressure, the thinning indirectly resulted in stand resilience because a third of the current understory established as a result of the 1998 thinning. Fifty regeneration plots located randomly over the 85 ha treatment area showed that of the 120 spruce per hectare on the site, 33% established as a result of the thinning. This post-thinning ‘catch’ of spruce suggests at least some spruce can be regenerated by treatments conducted prior to beetle-caused overstory mortality. Had the treatment been conducted even a few years earlier there would have likely been much more spruce regenerated prior to the outbreak. Furthermore, had there been more thinning treatments across the landscape, islands of spruce regeneration would have been maintained, which could have contributed to future spruce forests.

In managing the aftermath of a landscape-wide outbreak such as the one on the Markagunt Plateau, we suggest a strategic and tactical approach incorporating both resistance and resilience (Table 6.2). Focus can be shifted to sustaining large tree character while re-introducing spruce to the site. Management can take advantage of other mature non-host species to maintain forest characteristics during the short- and mid-term while spruce is reintroduced by planting for the long-term. If relatively shade-intolerant species (e.g., aspen (*Populus tremuloides*), lodgepole pine, or Douglas-fir (*Pseudotsuga menziesii*)) are present on the landscape they could be promoted to increase

the representation of early successional forest and increase the overall compositional heterogeneity on the landscape. However, potential disturbances associated with these forest types exist (e.g., ungulate herbivory in aspen (see Chapter 5), Douglas-fir beetle (Campbell et al. 2005), mountain pine beetle (Fettig et al. 2007)) and must also be taken into consideration.

Post-outbreak planting is almost certainly going to be part of any management plan to mitigate the effects of a spruce beetle outbreak. Therefore, collection and storage of Engelmann spruce seed from a range of appropriate seed zones should be a priority. Traditionally, seed would not be used if it came from seed zones that are lower in latitude or elevation. However, recent and rapid shifts in climate have resulted in the potential that genetic stock will not match seed collection areas (McKenney et al. 2009). Determination of seed zones might need to consider the historic and predicted future trends of increasing temperature so that collected seed will be matched to potential growing conditions. Finally, remember that planting the entire forest during a short period of time will result in a nearly even-aged spruce forest and/or landscape, hastening future beetle outbreaks.

Strategic planning to maintain spruce on the landscape, by promoting resistance and/or resilience to spruce beetle outbreaks, will not necessarily reduce the hazard for other disturbances such as stand-replacing fires. Trade-offs associated with this kind of management should be explicitly acknowledged throughout the planning process. In most spruce systems, spruce beetles are an ever-present threat and cause varying levels of mortality more frequently than stand-replacing fires (Schmid and Hinds 1974). Furthermore, stand-replacing fires in high elevation, moist spruce-fir forests are rare and,

when they do occur fire suppression is difficult. Therefore, preventive management based on maintaining Engelmann spruce forests should favor activities to mitigate spruce beetle outbreaks. Furthermore, although recent spruce beetle outbreaks are unprecedented they are not yet occurring everywhere in the West. To maintain perspective, the spruce beetle has only been detected on a relatively small percentage of the geographically unbiased Forest Inventory and Analysis plots in the Intermountain West (Figure 6.3).

Conclusions

To satisfy the objectives for maintaining spruce over the long-term in the face of likely beetle outbreaks silvicultural activities should focus on building resilience. We suggest management for direct control of spruce beetle outbreaks on a stand-by-stand basis probably has limited application. Similarly, activities that build stand resistance, although possible, have limited applicability for influencing spruce beetle outbreaks in the long-term. However, activities which promote resilience, i.e., increasing spruce age class diversity and tree species diversity across the landscape are possible, and will potentially mitigate future beetle outbreaks and maintain Engelmann spruce forests in the long-term.

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Table 6.1. Stand and landscape characterization of Engelmann spruce forest resistance and resilience to the spruce beetle

	Resistance	Resilience
Stand	Low probability of high beetle population levels arising from <i>within</i> the stand ^a	Vegetation response to an outbreak includes the maintenance of: <ol style="list-style-type: none"> 1. Mature stand character 2. Mature spruce 3. Potential for future spruce dominance
Landscape	Low probability of beetle transition from endemic to epidemic	<ol style="list-style-type: none"> 1. Maintenance of mature stands 2. Maintenance of spruce-dominated stands

^a Low susceptibility to attack (tree and stand)

Table 6.2. Stand and landscape attributes of Engelmann spruce forests that are resistant or resilient to the spruce beetle

	Resistant	Resilient
Stand	<ol style="list-style-type: none"> 1. High percentage of non-host species 2. Low relative densities 3. Small host size 	<ol style="list-style-type: none"> 1. Low percentage of host species 2. Low percentage of host species 3. Abundant young spruce
Landscape	High proportion of resistant stands	<ol style="list-style-type: none"> 1. Tree species diversity 2. Age class diversity of spruce



Figure 6.1. Establishment cut of shelterwood regeneration method in Engelmann spruce on the T.W. Daniel Experimental Forest in northern Utah.

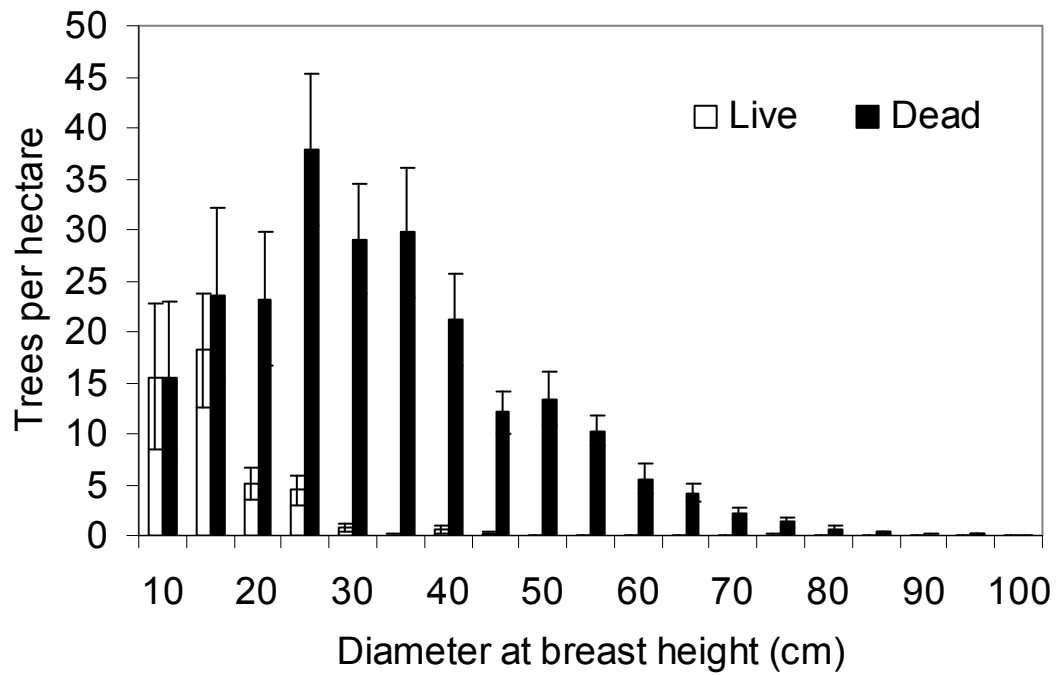


Figure 6.2. Engelmann spruce composite diameter distribution for all sites ($n=14$) on the Markagunt Plateau showing the drastic reduction in diameter of live spruce as a result of the outbreak. Only trees that were live prior to the outbreak were used to construct the distribution.

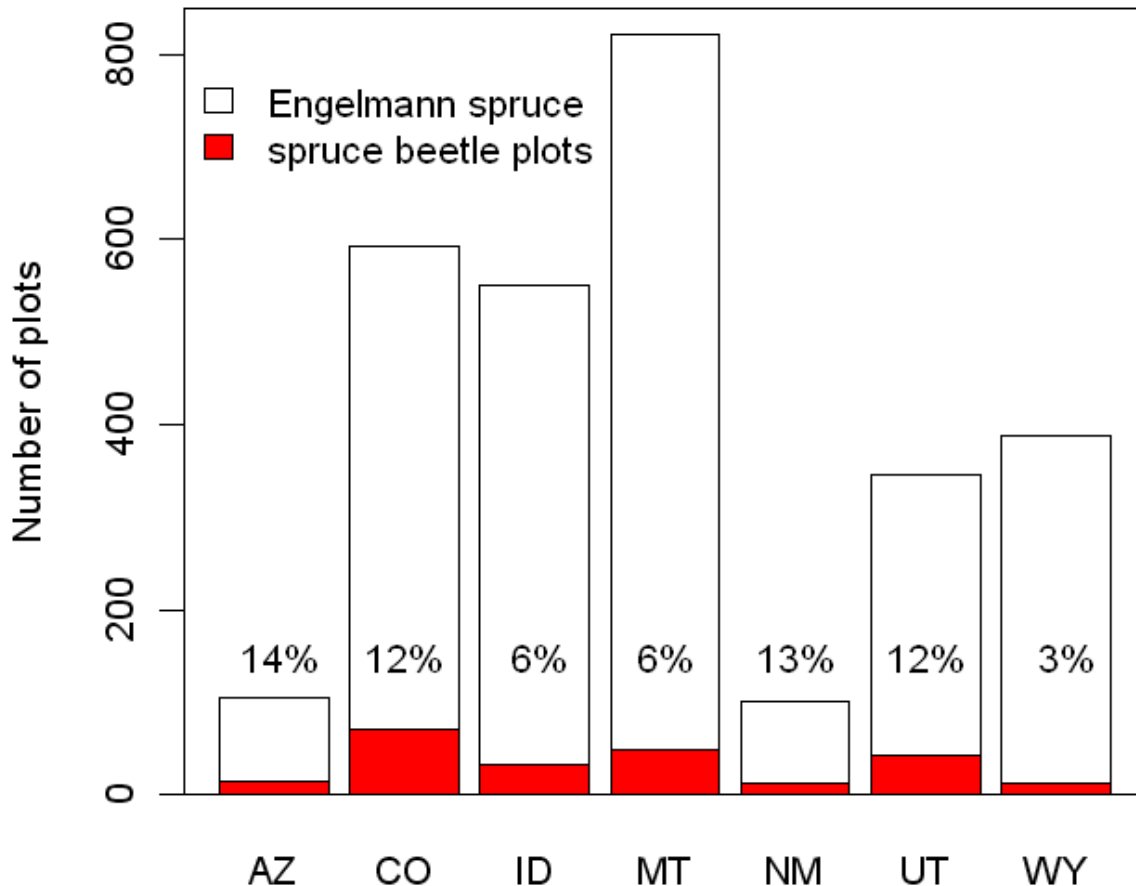


Figure 6.3. Number of plots with Engelmann spruce present by state in the Intermountain West juxtaposed with Engelmann spruce plots with spruce beetle (in red). Percentage of total Engelmann spruce plots with spruce beetle by state is indicated. The four corners states appear to be disproportionately affected. Data from USDA Forest Inventory and Analysis. Nevada not included (6 plots, 0 with spruce beetle).

CHAPTER 7

SUMMARY AND CONCLUSIONS

The disturbance ecology of spruce beetle-killed Engelmann spruce forests in the southern Rocky Mountains was explored. Using dendroecological methods we assessed the influence of antecedent disturbances in shaping the forests that ultimately succumbed to the spruce beetle outbreak and discovered a possible mechanism for the co-existence of spruce and subalpine fir in these communities. Spatiotemporal dynamics of beetle spread during the outbreak were found to exhibit spatial synchrony and were influenced by host and environmental conditions, and likely anomalies in the local climate. Post-outbreak forests were found to exhibit reduced potential for extreme wildfire behavior contrary to anecdotal observations in the literature. Forest response to the outbreak was found to be dominated primarily by the seedling bank, which is composed primarily of subalpine fir. Taken together, the new knowledge accumulated as a result of examining these dynamics resulted in a novel approach considering resistance and resilience to beetle outbreaks in the context of ecosystem management.

Antecedent disturbances

In light of the recent (1990s), landscape-wide spruce beetle outbreak on the Markagunt Plateau, it was postulated that the antecedent disturbance might have been a previous landscape-wide spruce beetle outbreak. However, multiple and consistent lines of evidence suggested mixed- and high-severity fire were the most likely antecedent disturbance. Furthermore, unlike the recent outbreak, the putative antecedent fires were spatially and temporally disparate in the period examined (1480-2000). Patterns of

establishment and subsequent stand development were related to the regional drought cycle, which helped to explain putative fire events and species-specific differential growth rates. We suggested it is likely the disproportional growth response to drought ultimately led to homogenous spruce conditions and increased host susceptibility prior to the recent outbreak. Furthermore, we suggested that this differential response to cyclical drought/pluvial conditions is a possible mechanism of spruce-fir coexistence.

Spatiotemporal dynamics

The spatiotemporal dynamics of the recent spruce beetle outbreak were strikingly similar to recent studies of other eruptive bark beetle species. In contrast to the common perception that spruce beetle outbreaks ‘move or spread’ across the landscape, we found spatial synchrony of multiple, building populations characterized the Markagunt Plateau outbreak. The variation in dates of death suggest that, while the heterogeneity of host conditions on the landscape and temperature anomalies both influenced spruce beetle populations, there are likely other factors that contributed to the observed spatiotemporal patterns. Future studies that combine the precision of dendrochronological approaches with the characterization of landscapes using appropriately sized pixels could further the understanding of eruptive bark beetle outbreaks.

Post-outbreak fire behavior

Simulations of potential fire behavior suggested Engelmann spruce forest structure and composition influenced the spruce beetle outbreak, which subsequently affected predicted fire behavior on the Markagunt Plateau. Interactions between the outbreak and subsequent potential fire behavior were related to Engelmann spruce composition: 1) at

sites with lower spruce composition the spruce beetle outbreak did not change canopy structure sufficiently to alter the potential for crown fire compared to pre-outbreak conditions; 2) at sites with high spruce composition the host-specific spruce beetle substantially reduced canopy fuel and therefore subsequent crowning potential for at least several decades; 3) in one site with a known surface fire history, the influence of the beetle outbreak on canopy fuel load may have had little or no net effect on subsequent potential fire behavior indicating a second-order disturbance interaction. Our results were consistent with interactions of spruce beetle and subsequent fire behavior with the results heavily influenced by pre-outbreak Engelmann spruce composition. We concluded that extreme fire behavior is not an inevitable consequence of spruce beetle outbreaks.

Forest reorganization

In sharp contrast to other high-severity disturbance types such as fire, the recent spruce beetle outbreak did not destroy the non-host overstory or seedling bank, nor did it create environmental conditions generally associated with the pulse regeneration of early seral species. Instead, the loss of the dominant overstory Engelmann spruce has opened growing space for the few non-host overstory species, where they occur, and released the seedling bank of primarily subalpine fir, which has been chronically regenerating for centuries. Although aspen exhibited a pulse in regeneration response to the outbreak it will not dominate post-outbreak stands because of intense browsing pressure. In this once Engelmann spruce-dominated landscape, the relatively few residual, non-host overstory trees will not be able to fully reoccupy the growing space; instead, the seedling bank will play the primary role in regeneration response. The chronically regenerating seedling

bank, typically associated with canopy gaps, created by low-severity disturbances, will dominate forest reorganization in response to the high-severity, host-specific spruce beetle outbreak.

Management for resistance and resilience

To satisfy the objective of maintaining spruce over the long-term in the face of likely spruce beetle outbreaks silvicultural activities should be focused on building resistance and/or resilience. We suggested management for direct control of spruce beetle outbreaks on a stand-by-stand basis probably has limited application on large landscapes. Similarly, activities which build stand resistance, although possible, also have limited applicability on large landscapes. However, activities which promote resilience, i.e., increasing landscape spruce age class diversity and tree species diversity are possible, and will potentially mitigate future beetle outbreaks and maintain Engelmann spruce forests in the long term.

CURRICULUM VITAE

Robert Justin DeRose**Personal Information**

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 Utah State University
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Education

Ph.D.	2006	Ecology	Utah State University
M.S.	2004	Forestry	University of Maine
B.S.	2002	Forestry	Utah State University

Teaching Experience

Invited Guest lecture: Introduction to dendrochronology for Climate Change WATS/CLIM 3820, March 25, 2008 and March 27, 2007. Introduction to dendrochronology for Historical Ecology WILD 6990, March 6, 2007, Utah State University.

Introductory Forest Stand Dynamics on the T.W. Daniel Experimental Forest: Utah State University, September 9 and October 7, 2006.

K-12 Instructor: Project Learning Tree workshop, Orono, ME, spring, 2004.

Teaching Assistant: Silviculture and silviculture lab FES 408/409, University of Maine; forest measurements, quantitative silviculture and growth and yield modeling (FVS), fall semester, 2002, 2003.

Professional Memberships

Candidate Certified Forester, Society of American Foresters
 Xi Sigma Pi
 Ecological Society of America
 Tree-Ring Society
 American Geophysical Union

Professional Recognition

First T. W. Daniel Graduate Fellow, 2005-2009
 Ralph H. Griffin scholarship for outstanding work in silviculture, 2004
 T. W. Daniel Undergraduate Forestry Scholarship, 2001

Competitive Grants and Funding as PI

DeRose, R.J., Long, J.N., and Shaw, J.D. Forest Health and Protection, Evaluation Monitoring, USDA Forest Service. Potential consequences of spruce beetle outbreaks on National Forests in Utah. \$15,000. 2008-2010.

DeRose, R.J. and J.N. Long. Ecology Center Research Support Awards (3). Disturbance ecology of Englemann spruce forests, 2008 (\$4,000), 2007 (\$4,000), 2006 (\$2,200).

DeRose, R.J. and J.N. Long. 2006. Intermountain Region Digital Image Archive Center Graduate Student Competitive Research Support Grant. Using Landsat Thematic Mapper to assess the spatiotemporal dynamics of a large-scale spruce beetle epidemic: quantifying forest structural attributes for outbreak forecasting. \$20,000.

Other Grants and Funding

DeRose, R.J., Long, J.N., and Shaw, J.D. Forest Inventory and Analysis Program, USDA Forest Service. Preliminary data analysis research proposal. \$30,000. 2009-2011.

DeRose, R.J., Long, J.N., and Shaw, J.D. Forest Inventory and Analysis Program, USDA Forest Service. Increment core archival and data analysis pilot proposal. \$50,000. 2009-2011.

Rittenour, T., L. Hipps, J.N. Long, R. Gillies, R.J. DeRose. 2009. Utah State University Water Initiative Research Initiation Award. Extending the record of drought and discharge variations in the Bear River drainage through tree-ring reconstructions: collection of initial data from the Logan River basin. \$19,930.

Ex, Seth, R.J. DeRose, and J.N. Long. 2008. Undergraduate Research & Creative Opportunities. Succession and stand development of *Cercocarpus ledifolius* woodlands in the Bear River Mountains, UT. \$500.

Ex, Seth, R.J. DeRose, and J.N. Long. 2008. College of Natural Resources, Utah State University. Succession and stand development of *Cercocarpus ledifolius* woodlands in the Bear River Mountains, UT. \$400.

Invited Presentations

Disturbance ecology of the Markagunt Plateau. University of Utah, Department of Geography Colloquium Series, Dec. 5, 2008.

Undergraduate Research Mentor

2008-2009: Seth Ex. Succession and stand development of *Cercocarpus ledifolius* woodlands in the Bear River Mountains, UT.

Refereed Publications

DeRose, R.J., and R.S. Seymour. 2009. The effect of site index on growth efficiency of upper crown class *Picea rubens* and *Abies balsamea* in Maine, USA. *Canadian Journal of Forest Research*. 39: 1-8.

DeRose, R.J., and J.N. Long. March 2009. Wildfire and spruce beetle outbreak: simulation of interacting disturbances in the central Rocky Mountains. *Ecoscience*. 16: 28-38.

DeRose, R.J., J.D. Shaw, G. Vacchiano, and J.N. Long. 2008. Improving longleaf pine mortality predictions in the Southern Variant of the Forest Vegetation Simulator. Third Forest Vegetation Simulator Conference, Ft. Collins, CO. Feb. 13-15, 2007. RMRS-P-54.

Vacchiano, G., J.D. Shaw, R.J. DeRose, and J.N. Long. 2008. Inventory-based sensitivity analysis guides calibration of the large tree diameter growth submodel of the Southern Variant of FVS. Third Forest Vegetation Simulator Conference, Ft. Collins, CO. Feb. 13-15, 2007. RMRS-P-54.

DeRose, R.J., and J.N. Long. 2007. Disturbance, structure, and composition: spruce beetle and Engelmann spruce forests on the Markagunt Plateau, Utah. *Forest Ecology and Management* 244: 16-23.

Submitted Manuscripts

DeRose, R.J. and R. Gardner. A technique to improve measurement of elusive tree ring boundaries in aspen (*Populus tremuloides* Michx.). *In press*. *Tree-Ring Research*.

DeRose, R.J. and J.N. Long. Regeneration response and seedling bank dynamics of a spruce beetle-killed Engelmann spruce landscape. *In press*. *Journal of Vegetation Science*.

DeRose, R.J., and R.S. Seymour. Patterns of leaf area index during stand development in even-aged balsam fir red spruce stands. *In revision*. *Canadian Journal of Forest Research*.

Sharik, T.L., Adair, W., Battaglia, M., Baker, F.A., Comfort, E.J., D'Amato, A., Delong, C., DeRose, R.J., Ducey, M.J., Harmon, M., Levy, L., Logan, J.A., O'Brien, J., Palik, B.J., Roberts, S.D., Rogers, P.C., Shinneman, D.J., Spies, T., Taylor, S.L., Woodall, C., and Youngblood, A. 7th North American Forest Ecology Workshop: Overview. *In revision*. *International Journal of Forestry Research*.

Reports

DeRose, R.J., Long, J.N., and Shaw, J.D. 2009. Potential consequences of spruce beetle outbreaks on Engelmann spruce forests in Utah. Final Report, Forest Health Monitoring Analysis and Reporting Program.

DeRose, R.J., J.N. Long, and J.D. Shaw. 2009. Relationships between forest structure, composition, site, and spruce beetle occurrence in the Intermountain West. In: McWilliams, Will; Moisen, Gretchen; Czaplewski, Ray, comps. 2008. Forest Inventory and Analysis (FIA) Symposium 2008; October 21-23, 2008; Park City, UT. Proc. RMRS-P-56CD. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 1CD.

University Service

2009: International grant proposal referee, Czech Science Foundation.

2007-2008: Department of Wildland Resources representative to the Graduate Student Senate, Utah State University.

2005-2007: College of Natural Resources Senator for the Graduate Student Senate, Utah State University.

2003-2004: Forest Ecosystem Science Departmental Representative to the Association of Graduate Students, University of Maine.

2001-2002: Forestry Club President, Utah State University.

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Signed *Lucia Jaeger*

Date October 26th, 2009

Fee